

Promotors

Prof. dr. ir. P. Goethals
Research unit Aquatic Ecology
Department of Applied Ecology and Environmental Biology
Ghent University

Prof. dr. ir. A. Mouton
Aquatic Management research unit
Research Institute for Nature and Forest
&
Research unit Aquatic Ecology
Department of Applied Ecology and Environmental Biology
Ghent University

Dean

Prof. dr. ir. G. Van Huylenbroeck

Rector

Prof. dr. Anne De Paepe

M.Sc. Ine Pauwels

Spatially explicit migration models of pike to support river
management

Thesis submitted in fulfilment of the requirements for the degree of Doctor
(PhD) of Applied Biological Sciences

Dutch translation of the title:

Ruimtelijk georiënteerde migratiemodellen voor snoek ter ondersteuning van het rivierbeheer

ISBN-number: 978-90-5989-723-6

Cover: Het oog van een snoek. Vilda foto's (www.vildaphoto.net)

This research was supported by the agency for Innovation by Science and Technology (Agentschap voor Innovatie door Wetenschap en Technologie; IWT)

The author and the promoters give the authorisation to consult and to copy parts of this work for personal use only. Every other use is subject to the copyright laws. Permission to reproduce any material contained in this work should be obtained from the author

Acknowledgements

“Close to the water, everything is happy”

-P. Salles, Brazilië 2013-

En dus begon ik enkele jaren geleden aan ‘een job in ’t water’ en aan een studie naar de interessante wezens die er in leven. Een hele mooie kans, die ik met beide handen greep. Een mooie kans om bij te leren over wetenschappelijk onderzoek, snoeken en modellen, maar nog veel meer over mezelf. Dit doctoraat bracht me geregeld tot de grenzen van men eigen kunnen, die ik heb kunnen verleggen met de hulp van enkele bijzondere mensen die ik hier graag voor wil danken.

In de eerste plaats wil ik mijn promotoren Prof. dr. ir. Peter Goethals en Prof. dr. ir. Ans Mouton bedanken voor hun wetenschappelijke ondersteuning en hun geloof in mij en dit werk.

Peter, bedankt om me de kans te geven om op jouw labo aan dit doctoraat te werken en dat zelfs langer dan voorzien. Het gevoel dat je van dag één (een gesprek over cellulaire automaten dat ik me nog levendig herinner) in mij geloofd hebt heeft me geregeld gestimuleerd om goed mijn best te doen en ook klaar te staan voor andere kleine labo-taken. Bedankt ook voor de kans om bij meer dan alleen dit onderzoek betrokken te zijn en voor de fijne ervaring in Kroatië. Het was soms moeilijk kiezen uit de verschillende mogelijke paden die je aanreikte, maar dat zie ik als een luxeprobleem.

Ans, ik vind haast de woorden niet om jou te bedanken voor de intense begeleiding, zowel wetenschappelijk als mentaal, non-stop vijf jaar lang op gezonde en ja zelfs minder gezonde dagen, op werkdagen maar even goed verlofdagen. Bedankt voor de duizend en één dingen die je me leerde en inzichten die je me gaf. Bedankt voor de kans om op het INBO te werken en om altijd klaar te staan met cruciale tips en gouden raad. Een wijze, bekende Zuid-Afrikaan zei ooit dat de glorie van het leven niet zit in nooit te vallen, maar telkens weer op te staan als je op de grond ligt. Bedankt dus ook om me telkens de moed en kans te geven om terug recht te staan als ik op de grond lag. Ik denk dat je getuige nummer één was van al mijn vallen en wederopstandingen en daarmee ook mijn ‘groeï als wetenschapster’. Ik kijk met mooie herinneringen (of was het ogen? Ja ge krijgt dien bak) terug op een heel fijne samenwerking. Laat me nog eens zwart op wit bevestigen dat je rol in de kwaliteit en het welslagen van dit werk wel degelijk heel groot was.

Het finaal afronden van dit werk bleek nog een pijnlijke steile helling op het einde van een lange tocht, terwijl een nieuwe tocht al begonnen was. Zonder de nodige ruimte tijdens het afronden van dit doctoraat was ik met grote waarschijnlijkheid nu nog onderweg. Ik wil mijn nieuwe baas, Johan Coeck, heel erg bedanken om me de laatste weken de ruimte te geven om dit werk af te ronden. Behalve onze chef, wil ik ook mijn collega’s hier voor bedanken. Ans, David, Emilie, Karen, Nico, Raf en Seb, Tom en Maarten, bedankt voor de steun en interesse in dit werk, voor de deugdelijke middagpauzes in ‘t Brusselse en toffe AB uitstappen. Geweldig dat ik dit niet moet achterlaten en jullie nieuwe collega mocht worden.

Een hele grote merci aan alle helpende handen in het veld. In de eerste plaats de telemetreerders van het eerste uur: Ans, Diego, Gert en grootvader, Joris, Pieter, Pieterjan, Nancy, Raf, Roland, Teis, Valérie, Vake en Youri. Daarnaast bedank ik ook Emilie, Raf, Seth en Yves voor het geweldige enthousiasme waarmee jullie van in de vroege uren het ijskoude Ijzer-water trotseerde om voor mij 15 snoeken te vangen. Zelfs de Vlaamse Roofvis Federatie kon aan jullie niet tippen. Niettemin ben ik ook hen dankbaar voor hun minder succesvolle poging.

Prof. dr. ir. Bernard De Baets, dr. ir. Jan Baetens en ir. Steffie Van Nieuland wil ik bedanken voor de samenwerking rond het modellerwerk en jullie waardevolle, kritische opmerkingen hierover. Jan, bedankt voor de begeleiding bij de eerste modellerstappen en de stappen richting Ben&Jerry's in Burlington. Steffie, je leverde een heel knappe bijdrage aan de modellering. Bedankt ook (samen met Joris) voor de fijne tocht door Noord-Amerika.

Het IWT Vlaanderen wil ik graag danken voor de financiële steun, zonder welke dit onderzoek niet mogelijk was.

Zonder centjes geen doctoraat, maar echt rijk wordt je pas van de warme steun en toeverlaat van liefvallige collega's, ondertussen vrienden te noemen. Laat ik beginnen met Gert en Pieter, mijn lelijke zusters en geweldige bureaugenootjes. Straf dat jullie mijn dagelijkse gekwetter overleefden. Heel erg bedankt allebei voor de vele fijne babbels, maar zeker ook voor jullie luisterend oor op moeilijker momenten. Sigrid, Veerle en Elina, een hele dikke merci voor de gigantische steun tijdens de laatste stresserende weken op het labo, ook buiten de vorm van crisistabletten en chocotoffen. Sigrid, een extra dank-je-wel voor alle administratieve hulp, meer dan 4 jaar lang. Dank ook aan alle andere collega's van het labo doorheen de jaren, voor de fijne babbels, koffiepauzes, het delen van de geneugtes van de taarten van Françoise en de legendarische team-building momenten.

Buiten het werk goed kunnen ontspannen, komt het werk alleen maar ten goede. Camping Oppuurs (ik doop het al tot traditioneel event bij deze), de winterse weekendjes, kerstboomverbrandingen en caféavonden zijn stuk voor stuk activiteiten die mijn leven kleur geven, daarom ook een welgemeende merci aan de vrolijke vrienden en vriendinnen uit Beurrem. Bijzondere dank aan Jean & Lotte, Dieter & Eva, Jeroen & Lotte, An, Helena en Dorien voor de babbels in moeilijker tijden.

Gelukkig kan je familie zelf niet kiezen, want ik had dat zelf nooit beter gekund. Om te beginnen een hele grote bedankt aan jullie, moeke en vake, voor de eeuwige steun en het geloof in mijn kunnen, om me mijn ding te laten doen al 28 jaar lang en een warme thuis te zijn. Ik krijg de tranen in de ogen als ik er aan denk. Allerliefste zus, merci om mij op tijd en stond met mijn beide voeten weer op de grond te zetten. Ook bedankt om telkens opnieuw ... uwe muziek stiller te zetten :-).

Bobon, bompa, Lien, Lena en co. Merci voor de fijne zaterdagmiddagen in de Boomstraat, het zaligste rustpunt van de week. Bobon, als ik op een dag zo'n grootmoeder kan zijn als jij, dan ben ik een gelukkige vrouw. Dank voor de tonnen liefde en goede zorgen, een geweldige bron van energie. Merci ook aan de fantastische Pauwels-bende voor de leuke familiemomenten. De optimistische en vrolijke manier waarop jullie allemaal in het leven staan inspireert me elke dag. Bijzondere dank aan mijn tante, Jeske Pauwels, voor de rustige werkplek en fijne verblijf in 't Gentse in het heetst van mijn schrijf-strijd.

Mijn lieve schone familie, in het bijzonder Lief en Roland, dank voor jullie geweldige steun bij dit werk op alle vlakken en om Teis en mij een warm nest aan te bieden in de Breevendreef. Sientje, (op de wereld gezet door Jeroen & Lotte ergens tijdens hoofdstuk 7), je meter heeft vanaf nu eindelijk meer tijd om samen leuke dingen te doen. Dank ook aan de Buysstraat en de familie in 'the far west' voor jullie interesse in mijn werk.

Dan rest er mij nog één hele grote (allergrootste) dank-je-wel uit te delen, en dit aan mijn allergrootste schat, Teis. Bedankt om mij telkens opnieuw de ruimte te geven om te doen wat ik graag doe, om mezelf en ons huisje zo goed te verzorgen op alle momenten dat ik meer "getrouwd" leek met mijn laptop dan met jou, en voor de tonnen en tonnen geduld en liefde. De verbouwing van onze chateau is het 3^e grote water dat wij samen glansrijk aan het overzwemmen zijn. Ik heb er nog nooit zo hard naar uitgekeken om hier terug samen aan voort te werken om er een gezellige thuis van te maken.

List of abbreviations

Vii

1 General introduction.....	1
1.1 Setting.....	1
1.2 Fish movement and migration.....	5
1.3 Pike ecology and qualitative and quantitative habitat relations	6
1.3.1 <i>Classification</i>	6
1.3.2 <i>Distribution</i>	7
1.3.3 <i>Habitat</i>	7
1.3.4 <i>Feeding</i>	9
1.3.5 <i>Life cycle</i>	9
1.3.6 <i>Qualitative environmental relations</i>	11
1.4 Pike status in Flanders.....	13
1.5 A road map to this thesis	17
2 Modelling fish migration	21
2.1 Introduction	21
2.2 Spatially explicit modelling	22
2.2.1 <i>Eligible modelling techniques</i>	22
2.2.2 <i>Conceptual aspects on IBMs</i>	23
2.2.3 <i>Conceptual aspects on CAs</i>	25
2.3 IBMs in fish migration modelling.....	27
2.4 CAs in fish migration modelling.....	29
2.5 Models on Northern pike <i>Esox lucius</i> L.....	29
2.6 Challenges and opportunities	30
3 Study area and data collection	33
3.1 Introduction	33
3.2 Fish telemetry.....	34
3.2.1 <i>Definition</i>	34
3.2.2 <i>Tag types and techniques</i>	34
3.3 Study area.....	40

3.4 Data collection.....	49
3.4.1 Adult pike capture and tagging	49
3.4.2 Pike tracking	51
3.4.3 Sampling of juvenile pike	57
3.5 Data analysis	58
4 Exploring the opportunities of the cellular automaton (CA) paradigm for pike migration simulation	59
4.1 Introduction	59
4.2 Modelling method	59
4.2.1 Study area and data.....	59
4.2.2 Model structure and assumptions	61
4.2.3 Transition rules.....	64
4.2.4 Carrying capacity.....	65
4.2.5 Model output and sensitivity analysis	68
4.3 Results basic model.....	69
4.3.1 Steady-state pike distribution.....	69
4.3.2 Number of iteration steps before convergence.....	71
4.4 Results further optimisation of the basic model.....	77
4.4.1 Steady-state pike distribution.....	77
4.4.2 Number of iteration steps before convergence.....	77
4.4.3 Scenarios	80
4.5 Discussion	81
5 Exploring the opportunities of individual-based modelling (IBM) for pike migration simulation	85
5.1 Introduction	85
5.2 Modelling method	86
5.2.1 Study area.....	86
5.2.2 Model development	86
5.2.3 Initial and boundary conditions	92
5.3 In silico experiments	94
5.3.1 Initial condition and side arms.....	94
5.3.2 An annual cycle	95
5.3.3 Validation of the simulation results	99
5.4 Discussion	101
6 Adult pike movement and migration.....	105
6.1 Introduction	105
6.2 Material and Methods.....	106
6.2.1 Study area and data collection.....	106
6.2.2 Data analysis.....	106
6.3 Results	109
6.3.1 Annual movement	109
6.3.2 Migration.....	109
6.3.3 Triggers for pike migration	110
6.4 Discussion	112
7 Adult pike habitat use and preference	115
7.1 Introduction	115
7.2 Material and methods	116

7.2.1 Study area.....	116
7.2.2 Data analysis.....	116
7.3 Results	119
7.3.1 Habitat use at the macro-scale.....	119
7.3.2 Habitat use at the meso-scale.....	120
7.4 Discussion	122
7.4.1 Habitat use at the macro-scale.....	122
7.4.2 Habitat use at the meso-scale.....	123
8 Habitat suitability model for adult pike in a lowland river.....	127
8.1 Introduction	127
8.2 Material and methods	129
8.2.1 Study area and data.....	130
8.2.2 Model structure	130
8.2.3 Model reliability and method selection.....	131
8.2.4 Variable selection.....	133
8.2.5 Rule base	134
8.3 Results	134
8.3.1 Model reliability and method selection.....	134
8.3.2 Variable selection.....	136
8.3.3 Rule base	138
8.4 Discussion	141
8.4.1 Model performance	141
8.4.2 Variable selection.....	142
8.4.3 Rule base	143
9 General conclusions and further research	145
9.1 General conclusions	145
9.1.1 CA-based model versus IBM to simulate pike migration.....	145
9.1.2 Adult pike ecology and management.....	146
9.1.3 Analysing pike movement data and habitat use	148
9.2 Indications for further research	149
9.2.1 CA-based model versus IBM to simulate pike migration.....	149
9.2.2 Adult pike ecology and management.....	149
9.2.3 Analysing pike movement data and habitat use	151
9.3 Contributions of this thesis.....	151
Appendix	153
References	159
Summary	177
Samenvatting	179
Curriculum Vitae	183

The following chapters were published in international peer-reviewed journals or submitted for publication in an international peer reviewed journal (A1).

Chapter 4 was published as:

Pauwels, I.S., Mouton, A.M., Baetens, J.M., Van Nieuland, S., De Baets, B. & Goethals, P.L.M. 2013. Modelling a pike (Esox lucius) population in a lowland river using a cellular automaton. Ecological Informatics 17: 46-57.

Chapter 5 was published as:

Baetens, J.M., Van Nieuland, S., Pauwels, I.S., De Baets, B., Mouton, A.M., Goethals, P.L.M. 2013. An individual-based model for the migration of pike (Esox lucius) in the river Yser, Belgium. Ecological Modelling 258: 40-52.

Chapter 6 was published as:

Pauwels, I.S., Goethals, P.L.M., Coeck, J., Mouton, A.M. 2014. Movement patterns of adult pike (Esox lucius L.) in a Belgian lowland river. Ecology of Freshwater Fish 23: 373-382.

Chapter 7 was submitted as:

Pauwels, I.S., Goethals, P.L.M., Coeck, J., Mouton, A.M. submitted. Habitat use of adult pike (Esox lucius L.) in a lowland river. Hydrobiologia.

List of Abbreviations

ACF	autocorrelation function
AF	artificial foreshore
AIC	aikake information criterion
AS	Autumn-Summer
AV	artificial vertical bank
B	bare vegetation/river bank type
BBK	brownian bridge kernel
CA	cellular automaton
CCI	correctly classified instances
CIW	coördinatiecommissie integraal waterbeleid
D	depth
GAM	generalized additive model
GAMM	generalized additive mixed model
GBM	group based model
GLMM	generalized linear model
GPS	global positioning system
H	high (as class in the crisp sets of chapter 8)
H ₂ S	hydrogen sulphide
HIC	hydrologisch informatie centrum
HSI	habitat suitability index
HSM	habitat suitability model
IBM	individual-based model
IdE	integro-difference equation
ID code	identification code
INBO	research institute for nature and forest research
L	low (as class in the crisp sets of chapter 8)
LHX	life history transmitter
LM	linear model
M	medium (as class in the crisp sets of chapter 8)
Ma	macrohabitat type
MDD	minimal average daily distance moved
O ₂	oxygen
ODD	overview design concepts and details protocol

OdE	ordinary difference equation
Op	open water
PAT	pop-up archival tag
PDE	partial differential equation
PdE	partial difference equation
PIT	passive integrated transponder
PSAT	pop-up satellite archival tag
R	reedy vegetation
Ri	riparian zone
S	season
Sa	side arm in the HSM
$S_{1-2} = \text{SG2-3}$	natural spawning grounds in this study area
$S_3 = \text{SG1}, S_{4-6}$	artificial spawning grounds in this study area
SNB	semi-natural bank
Sp	Spring
STDEV	standard deviation
T_{1-4}	the four main tributaries of the river Yser: Handzamevaart, Kanaal Ieper-IJzer, Kemmelbeek, Boezingegracht, respectively
TTI	time to independence
Tr	tributary in the HSM
V	vegetation type
VHF	very high frequency
VIF	variance inflation factor
VL	very low (as class in the crisp sets of chapter 8)
VMM	Flemish environment agency
W	woody vegetation
Wi	Winter
YCF	year class formation
YCS	year class strength
YOY	young-of-the-year

CHAPTER 1

General introduction

1.1 Setting

Last decades, substantial efforts are made in Flanders (Belgium) to enhance the ecological river quality. These efforts have largely and successfully concentrated on improvement of the chemical water quality (CIW 2010). Notwithstanding, the biological quality is still far from the intended standard set by the European Water Framework Directive (EU 2000) and many aquatic species have not regained a healthy status (Verreycken et al. 2012, VMM 2012). The greatest cause so far beside the moderate water quality, is a lagging habitat quality by habitat deterioration and fragmentation.

Aquatic species that are mostly affected by habitat degradation and fragmentation are definitely fish and specifically migratory fish. The habitats that migratory fish use to feed, rest, hide and reproduce may be very dispersed making free migration between these habitats essential to survive (Northcote 1978). However, a historically unbalanced interest in favour of shipping and agriculture led to canalisation by straightening and deepening of rivers and creation of dams, sluices, valves and other hydraulic constructions, which control the water level, drain potential suitable habitats and obstruct fish migration (Monden 2007).

Therefore, river managers in Belgium and in the rest of Europe plan and execute measures to conserve and restore the river habitat and enhance the accessibility (CIW 2010) by for instance remeandering, floodplain creation, bank restoration and creation of fish passages. As such, the Flemish government planned to reduce the number of fish migration barriers of first priority with 90% by December 31st 2015 (1st phase) and the other 10% by December 31st 2021 (2nd phase; CIW 2010; www.integraalwaterbeleid.be). The success of these management plans requires an efficient allocation of the efforts beside an assessment of the impact of each measure on river ecology. Therefore, good knowledge on the status of the aquatic system, the main bottlenecks and the ecology of the target species is essential. Integrating this knowledge in models can help to quantitatively predict the impact of a specific measure and may help to better understand the habitat requirements and spatial dynamics of the fish.

Habitat suitability and species distribution models have already proven to be valuable tools (Gillenwater et al. 2006, Mouton et al. 2009a, Mouton et al. 2009a, Mouton et al. 2008a, Mouton et al. 2007, Mouton et al. 2009b, Mouton et al. 2012b). These models predict the presence or abundance of species based on key habitat characteristics by different modelling techniques, such as artificial neural networks (Lek & Guegan 1999), decision trees (D'heygere et al. 2003, 2006), fuzzy logic (Adriaenssens et al. 2004a, Adriaenssens et al. 2006, Mouton 2008), logistic regression (Willems et al. 2008) and Bayesian belief networks (Adriaenssens et al. 2004b, Landuyt et al. 2013). These modelling techniques are helpful tools in understanding the suitability of local, critical habitat variables such as water depth, flow velocity and vegetation characteristics. However, they do not allow to model population viability constraints by wider, large scale variables, such as recruitment and migratory access (Mcdowall 1993). Since it is likely that these variables constrain the abundance of migratory species more than local habitat variables, habitat suitability models for fish should take into account factors relating to migration and accessibility (Hayes et al. 2009). Therefore, models should account for spatial and temporal processes (e.g. migration) over only spatial (e.g. local habitat variables) or only temporal processes (e.g. population growth).

We illustrate the importance of accounting for spatial and temporal processes beside only spatial processes by comparing the predicted suitable area in a spatial model with the predicted suitable area in a spatial-temporal model in four different scenarios (Figure 1-1). Two of these scenarios (scenario 2 and 4 in Figure 1-1) represent a potential river management question on the enhancement fish migration from the main river to the tributaries (scenario 2) and the rehabilitation of river bank habitat (scenario 4). All scenarios represent a river and one tributary by a grid of cells. Each cell indicates the habitat suitability, being bad or good for juvenile pike that were assumed to be born in the tributary.

In the first scenario free migration from and to the tributary is possible and the habitat suitability remains constant. The scenario illustrates that accounting for migration processes indicates that juvenile pike could never reach the potential suitable habitat at the distinct location in the main river because it is too far. Consequently, the proportion of suitable area is smaller than would be predicted when migration was not accounted for (Figure 1-1).

In the second scenario a check valve is present at the outlet of the tributary blocking free migration to the tributary most of the time. However, when the area inundates free migration is restored. The habitat suitability remains constant. This scenario indicates that only by accounting for migration processes it is possible to account for the effect of the check valve on the proportion of suitable habitat (Figure 1-1).

In the third scenario free migration from and to the tributary is possible, but the habitat suitability for juvenile pike depends on the time. In spring the juveniles hide and grow up in the submerge vegetation where they were born, whereas in winter they migrate to areas with emergent vegetation. Only by simulating temporal processes beside local interactions, the effect of a changing habitat suitability on the proportion of suitable habitat is accounted for (Figure 1-1).

In the fourth scenario, a certain length of the river bank is rehabilitated. The rehabilitation may be performed in two different ways. In one way the rehabilitated bank is not spatially separated, whereas in the other situation it is. Although the total length of the rehabilitated bank is equal for the two methods, only one method may enable usage by juvenile pike from the tributary; This may only be discovered when the habitat suitability model accounts for time and migration processes.

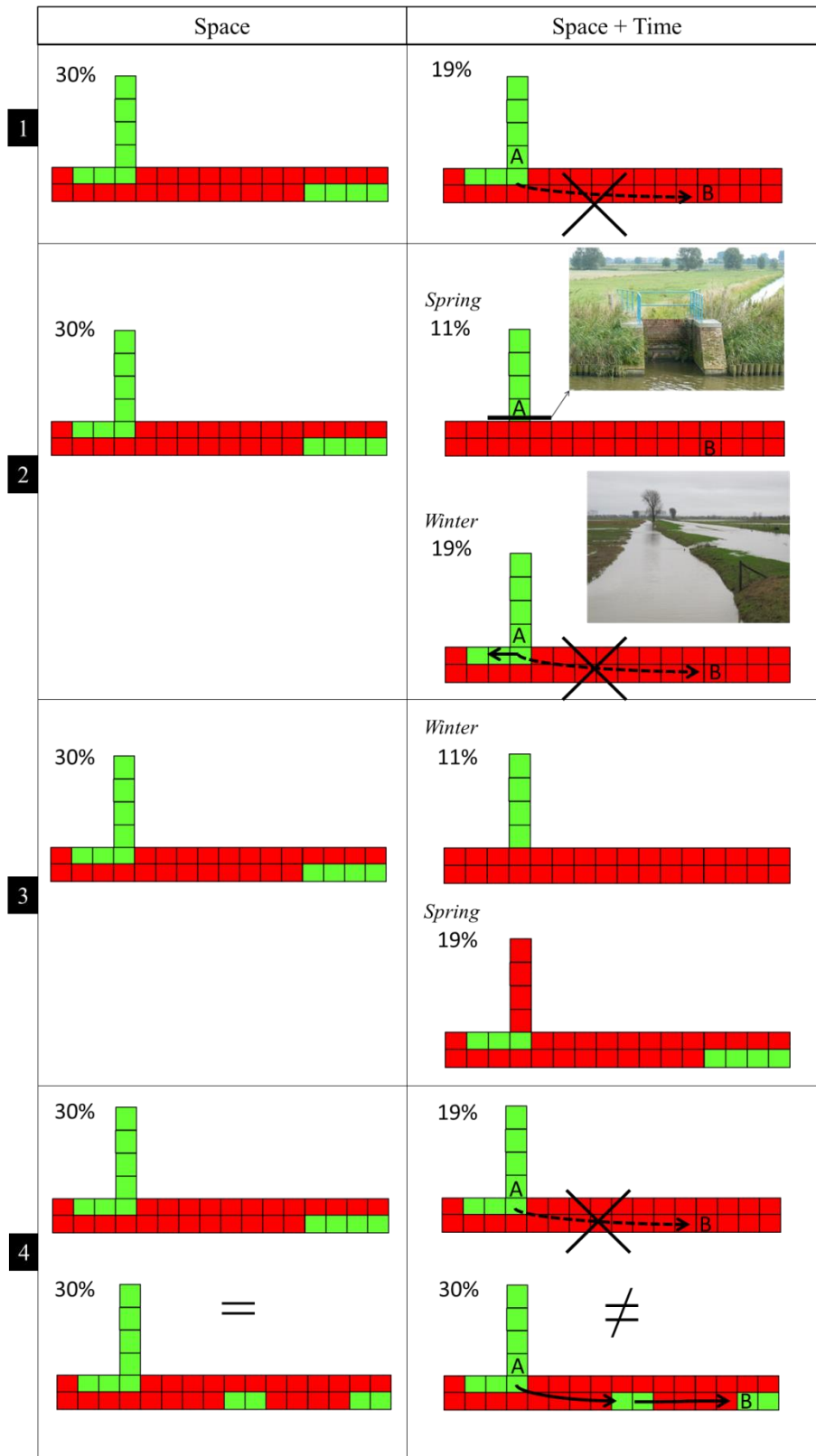


Figure 1-1: Illustration in four scenarios (1-4) of the benefit of accounting for space and time (right hand side) over only space (left hand side) in pike models supporting river management. In all scenario's the grids represent a hypothetical river and its tributary (green cells: suitable juvenile habitat., red cells: unsuitable juvenile habitat). It is assumed that pike were born in the tributary and may migrate from the tributary (A) to the main river (B). Percentages indicate the predicted proportion of suitable habitat.

Two interesting modelling techniques that may account for space and time are individual-based models (IBMs) and cellular automata (CAs).

IBMs allow to model the dynamics of individuals in an ecosystem that shows non-uniform variation of environmental variables (Perry & Enright 2007), and therefore have been applied frequently in this context (Le Fur & Simon 2009, Li et al. 2010, Uchmanski et al. 1999, Yemane et al. 2009). An IBM considers each fish as an individual of which the condition and position are tracked in time based on characteristics such as gender, age and a limited set of environmental variables.

CA models are similar to IBMs but focus on the effect of spatially and temporally heterogeneous environmental conditions on the population, rather than on the individual characteristics and behaviour. Characteristic of CAs is the discrete nature of the time, space and state domains. CAs allow for transparent modelling of complex systems based on simple transition rules and are flexible in incorporating individual differences and local interactions. Since river managers are more interested in the impact of environmental changes on entire populations than on individual fishes, CA models may be more appropriate than IBMs to support river management and to reveal effective rehabilitation measures. However, they were not often applied in this respect (see chapter 2). In contrast, IBMs have already been widely used to model fish migration and population abundance (chapter 2; Bauer and Klaassen 2013, Hubbard, et al. 2004, Weber, et al. 2006).

The aim of this PhD is to support river management with knowledge on northern pike *Esox lucius* L. ecology and the spatially explicit modelling of pike migration. Specifically, we aimed to provide insight into:

- the applicability of the IBM and CA modelling paradigms to simulate adult pike migration and eventually assess the effect of river rehabilitation options on fish;
- the movement and migration dynamics, and the habitat use and preference of adult pike in a lowland river;
- the methodology to properly evaluate the habitat use and preference of migratory fish.

Therefore, field data were collected by radio telemetry in the river Yser. The data were analysed to evaluate pike's movement and migration dynamics and its habitat use and preference. The results were further evaluated by a preliminary rule-based habitat suitability model for adult pike in a lowland river. Beside the use of the field data for model development the data were used to directly support river management with knowledge on adult pike migration dynamics and habitat use.

The focus of this thesis is on northern pike, but the concept of the modelling method applies to decision support in river management in general and could be applied on other fish species as well. Pike was used as a good representative for potamodromous fish species. It is a cannibalistic predator on top of the food chain that has specific habitat requirements (Craig 1996). Although it is not threatened neither vulnerable in Flanders according to the IUCN red list (Verreycken et al. 2012), its status has declined from the fifties to the nineties and pike did not regain its former status. To rehabilitate pike populations, successful conservation actions are needed. Hence, information on its spatial and temporal dynamics and thus information on its migration dynamics, its habitat use and preference, the limiting environmental factors and the spatial distribution of the preferred habitats is essential.

Fishing campaigns between 1998 and 2002, and between 2007 and 2012 revealed that the basin of the river Yser contained the highest pike density relative to the other 11 basins in Flanders (www.vis.milieinfo.be). Furthermore, the river Yser is one of the biggest rivers in Flanders having a naturally reproducing pike population and recently bank rehabilitation actions were performed that have not been evaluated yet for adult fish. Therefore, we selected the river Yser as study area to collect data on adult pike.

Further in this introduction we define fish movement and migration (section 1.2). Next, we give an overview of the ecology of northern pike in section 1.3. Its ecology and life cycle has already been described multiple times and the relation to the environment of life processes and stages has been thoroughly investigated (Bry 1996, Casselman 1978, Casselman & Lewis 1996, Craig 1996, Craig 2008, De Laak & van Emmerik 2006, Inskip 1982, Raat 1988b), therefore we keep the overview brief and refer to previous research on pike ecology for more detailed information, specifically on the qualitative and quantitative relations with environmental variables. In section 1.4 we evaluate the status of pike in Flanders. Lastly, the thesis outline is given in section 1.5, with a clear link to the life cycle of pike.

1.2 Fish movement and migration

As for most animals, the migratory behaviour of fish follows from the dispersion of the habitats that they use to feed, rest, hide and reproduce (Northcote 1978). Some of these habitats are in a localised area and exhibit daily movements, whereas others are further away and cause seasonal patterns of movement associated with variable resource utilisation (Lucas et al. 2001). For instance eggs hatch at the location where their parents migrated to for spawning and soon after hatching the larvae will migrate passively or actively to their first feeding habitat, which can be a few meters to thousands of kilometres away depending on the species. The larvae grow up to juveniles and subsequently need different food or less coverage from vegetation, so they migrate to a juvenile feeding habitat. At changing conditions, e.g. harsh winter conditions, the juveniles may move again to other habitat where survival success is higher. In most species, the oldest juveniles subsequently make a third migration event to other grow and feeding habitat that they had never exploited before. After maturation, the adults will exhibit spawning migration for the first time, in which they leave the survival habitat to move to suitable reproduction habitat (Coeck 2002). This cycle of daily movements between feeding and resting habitat, and seasonally migrations between growing and survival habitat can happen yearly for many years or only once depending on the species and the circumstances.

Where fish (or other animals) restrict their activities to a well-defined region of space, this is commonly termed the ‘home range’ or ‘home area’. Longer range exploratory movements and dispersal processes may enable areas with better resource characteristics to be discovered and utilised, and may result in the adoption of new home ranges (Lucas et al. 2001).

In conclusion, movement and migration are defined differently. Generally it is agreed that **migrations** are synchronised movements that are large relative to the average home range, predominantly directional, occurring at specific stages of the lifecycle and meant to increase the reproductive success, whereas **movements** are the daily displacement between resting, hiding and foraging habitat and are therefore short-distance and less directional (Lucas et al. 2001, Northcote 1978). Most of the studies that have been devoted to research questions of pike movement so far analysed patterns of daily displacement. As stated by Northcote (1978), migration aims to increase the reproductive success and is thus not necessarily movement over a long distance.

In this PhD research we define short distance displacements as movement and assume these represent the daily displacements of the fish between their resting, hiding and foraging habitat, whereas the long distance displacements are defined as migrations, assumed to be displacements for reproduction. It is important to bear in mind this definition while reading section 3.5.1 and chapter 6 of this thesis.

1.3 Pike ecology and qualitative and quantitative habitat relations

Pike is a top predator with very specific and varying habitat requirements for feeding and spawning during the year. It is a keystone piscivore in slow flowing and still freshwater habitats of the northern hemisphere that can influence species composition, abundance and distribution of other species in the community, including other pike by cannibalism and competition (Craig 2008).

Pike typically has a long, flat, 'duck-bill' snout (Figure 1-2), a large mouth with many large, sharp teeth and a dorsal and anal fin that is positioned rearward (Kottelat & Freyhof 2007, Morrow 1980). Gill rakers are present only as patches of sharp teeth on the gill arches. The lateral line is notched posterior (Morrow 1980). Pike's dorsal fin is located far to the rear and its anal fin is located under and arising a little behind the dorsal fin. The pectoral and pelvic fins are low on the body and the pectorals' base is under the opercle. Further, the paired fins are rounded and paddle-shaped (Morrow 1980) and the caudal fin has 19 rays (Spillman 1961). The colour of its body can vary from green to grey depending on the habitat. Also, the stripe pattern and spots on the flanks varies with the environment and condition. The belly is yellowish white. Female pike can be up to one and a half meter long. Male pike grow slowly and are rarely more than one meter long (Vandelannoote et al. 1998).



Figure 1-2: Image of Northern pike (*Esox lucius* L.) by Gino Meskens.

1.3.1 Classification

Northern pike *Esox lucius* L. is a ray-finned fish (Actinopterygii) that belongs to the order of the pikes and mudminnows (Esociformes) and the family of the pikes (Esocidae):

- Kingdom: Animalia
- Phylum: Chordata
- Subphylum: Vertebrata
- Superclass: Osteichthyes
- Class: Actinopterygii
- Order: Esociformes
- Family: Esocidae
- Genus: *Esox*
- Species: *lucius*

The genus *Esox* contains five species beside the species *lucius*: *E. americanus americanus*, *E. americanus vermiculatus*, *E. masquinongy*, *E. niger* and *E. reichertii*. None of these species occurs in Europe. The first four species live in North America, whereas the latter occurs in Asia (www.fishbase.org).

1.3.2 Distribution

In Europe, northern pike is absent in Iceland, North Scotland, South Serbia, the West and North of Norway, Spain, Portugal, Greece and the South of Italy. In America northern pike occurs in the North of the United States, South Canada and Alaska, and in Asia it occurs in the South of Russia and Siberia, Azerbaijan, Georgia, Armenia, Kazakhstan, Uzbekistan and Turkmenistan (www.fishbase.org; Figure 1-3).

In Ireland pike occurs since the middle ages due to stockings. In Germany, the species is considered vulnerable and pike mainly occurs thanks to stocking programmes. The former follows from habitat degradation due to river embankment and artificial water level management.

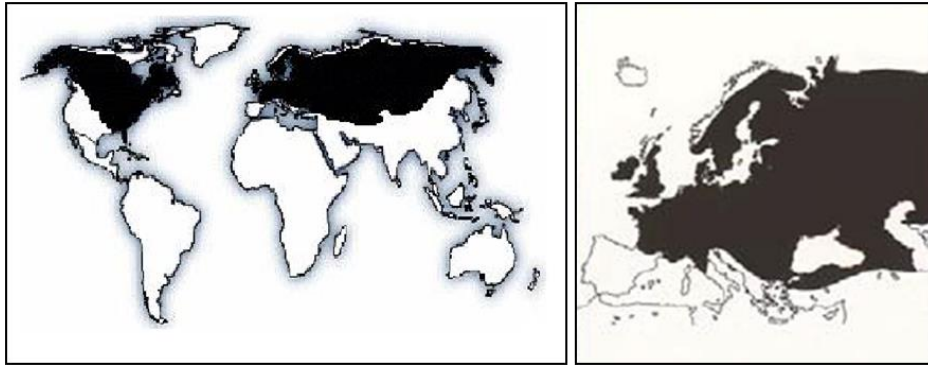


Figure 1-3: Distribution of pike (*Esox lucius* L.) in the world (left) and in Europe (right; Maes et al. 2004).

1.3.3 Habitat

Pike can tolerate a wide range of environmental conditions but are primarily cool-water fish (mesothermal) that best adapt to shallow (< 12m), slow flowing or stagnant and productive, mesotrophic-eutrophic environments (Casselman & Lewis 1996, Craig 1996). Although pike are freshwater fish, adult pike may tolerate brackish water. Pike were for instance observed in the Baltic Sea, which is brackish due to salt intrusion from the North Sea (Jacobsen et al. 2007).

The species is partially phytophilous, meaning that it depends on vegetation for parts of its life (Inskip 1982). Specifically, eggs, larvae and juveniles are vegetation bound, but also adults need vegetation to hide, rest and hunt and are thus seldom further than a few hundreds of meter away from vegetation (Chapman & Mackay 1984a, b, Inskip 1982).

In a telemetry study in 1951 by Rawson in the Great Slave Lake in North Canada (Inskip 1982) more than 90% of the tagged pike were observed within 400 m from the shore. Only few fish were observed in water of 10 m depth. It is hypothesised that the distribution of pike is determined by the effect of depth on the water temperature, the oxygen concentration, vegetation and pikes' prey. Telemetry studies in the first half of the twentieth century have indicated that pike seldom moves below the thermocline in stratified lakes (Inskip 1982).

The occurrence of pike close to the vegetation and its movement rate between shore and open water may also shift with seasons. Kobler et al. (2008a, 2008b) observed tagged pike on average closer to shore in winter than summer and observed small pike on average closer to

shore than large pike. He furthermore suggests that movement to and from shore depends on the migration of the prey and observed pike more in open water during the night and in the vegetation near shore during the day. In a similar study, Cook and Bergersen (1988) found a similar daily movement pattern from and to shore. However, some controversy still exists on the distance to shore in summer and winter. Several authors observed that a larger distance to shore in winter than summer, which is the opposite of Kobler's observation (Cook & Bergersen 1988, Craig 1996, Diana et al. 1977, Jepsen et al. 2001). It is believed that the differences are due to differences in prey availability, structure of the bank and the available vegetation during ice-out in winter (Kobler et al. 2008a, Kobler et al. 2008b).

It is unknown what the minimal surface area is of a water body to successfully sustain a naturally reproducing pike population. Information on the sustainability of a one hectare of water body substantially varies from 2.5 and 8.3 to 200 adult pike (or 4 to 15 kg; Craig 1996) and 40 to 50 and 1.1 to 1.6 adult pike (Margenau et al. 2008).

The relation between the maximal sustainable pike biomass and the percentage of vegetation cover has been studied thoroughly by Grimm (1996) in stagnant water. The rules that underlie the relation are investigated for the following types of water bodies: (1) a water body without submerge vegetation, (2) a relatively small water body with 80 % submerge vegetation cover and (3) a relatively small water body with 100 % submerge vegetation cover. The rules are an indication of the theoretical total pike biomass in the water body. In practice, the biomass may deviate from the theoretical estimation by the way the vegetation is distributed, the turbidity of the water, the surface area of the water body and influences on the prey density. A pragmatic maximal pike biomass of 150 kg.ha⁻¹ was considered while determining the rules, and a higher pike biomass was considered unrealistic due to intraspecific competition (Grimm & Klinge 1996). For all three types of water bodies pike biomass linearly increases with vegetation cover (Table 1-1).

Table 1-1: Quantitative relation of pike biomass and percentage of vegetation cover in three types of water bodies (Grimm & Klinge 1996).

Type of water body	Rule
No submerge vegetation	$4.8 \text{ kg pike} \times \frac{1 \% \text{ emergent vegetation cover}}{1 \text{ hectare}},$ <p>based on:</p> <ul style="list-style-type: none"> - 80-150 kg of 0-54 cm pike per hectare of emergent bank vegetation¹ - Biomass of > 54 cm pike in open water² negatively correlated to 0-54 cm pike near the bank
80 % submerge vegetation cover	$7 \text{ kg pike} \times \frac{1 \% \text{ emergent vegetation cover}}{1 \text{ hectare}},$ <p>where the extra 2.2 kg biomass per percent vegetation per hectare compared to water bodies without submerge vegetation is following from an increase of 25-43 cm pike.</p>
100 % submerge vegetation cover	$3 \text{ to } 6 \text{ kg } 0 - 54 \text{ cm pike} \times \frac{1 \% \text{ emergent vegetation cover}}{1 \text{ hectare}}$ <p>No pike of > 54 cm length are expected to live in water bodies that are fully covered with submerge vegetation.</p>

1: The standard definition of bank vegetation is vegetation within two meters (lakes) or one meter (canals) of the bank.

2: Open water is every location at more than two meters (lakes) or one meter (canals) of the bank.

1.3.4 Feeding

Adults are visual predators that hunt using an ambush sit and wait strategy. They hide between the vegetation till their prey passes by to catch it (Craig 1996). Nevertheless, blind pike and pike in very turbid water may also survive by hunting with the sensor organs in their lateral line (De Nie 1996). Most studies on pike's diet are conducted in North America (Beaudoin et al. 1999, Diana 1979, Sammons et al. 2011) and Canada, so the results are only partially comparable to European pike, but generally they show a high trophic flexibility (Chapman & Mackay 1990, Chapman et al. 1989).

Pike start eating exogenous food as soon as they enter the larval stage. This is immediately after the egg stage, when food is provided by the yolk. The diet of the larvae consists mainly of mosquito larvae (Chironomidae), water fleas (Cladocera), copepods (Cyclopoida) and ostracods (Ostracoda). As the larvae grow they start eating bigger prey, such as isopods (Asellidae) and amphipods (Gammaridae). Although the larvae may already be cannibalistic, most pike start eating fish of other and the same species between 4 and 8 to 15 cm according to Craig (2008). Some pike continue to live on a diet of Gammaridae and other macroinvertebrates, making them grow more slowly than their piscivorous counterparts. As such, a bimodality may occur within the young-of-the-year (YOY) population class (De Laak & van Emmerik 2006).

Usually, pike predate the most dominant prey species of the water body, which often is white bream (*Blicca bjoerkna* L.), roach (*Rutilus rutilus* L.), European eel (*Anguilla anguilla* L.), freshwater bream (*Abramis brama* L.) and common carp (*Cyprinus carpio* L.) in this region (Flanders, Belgium). Two dominant predators beside pike that may also be eaten by pike are European perch (*Perca fluviatilis* L.) and pikeperch (*Sander lucioperca* L.). In one study in Estland pike's diet mainly existed of ruffe (*Gymnocephalus cernua* L.), European smelt (*Osmerus eperlanus* L.) and European perch (*Perca fluviatilis* L.; Raat 1988). Generally, the choice of prey will depend on several factors, such as the preference of the predator, the vulnerability of the prey and their density and diversity. Furthermore, several predator-prey reactions exist that may affect pike's diet. As such the Crucian carp (*Carassius carassius* L.) may develop a higher body height in the presence of pike through the notion of alarm substances (specific hormones/chemicals; Craig 1996) and sticklebacks may behave passively when noticing similar alarm substances, indicating the presence of pike (Gelowitz et al. 1993).

When the common fish species get less abundant or diversity is very low, pike may switch to eating animals of a lower trophic level such as macroinvertebrates, amphibians, and small mammals, such as rats, mice and small waterfowl (Beaudoin, et al. 1999, Diana 1979, Sammons, et al. 1994). Low prey availability, high density of large pike and low vegetation cover may also increase the rate of cannibalism (Craig 1996). Cannibalism already occurs in the larval stage. At low prey availability, larvae of up to 3 cm may already eat conspecifics and cannibalism may rise to 40 % among larvae and juveniles (Raat 1988b). Young pike react to the moving tail of smaller pike (12-17 mm) and try to catch it by positioning themselves behind the fish (De Laak & van Emmerik 2006). Adults may swallow conspecifics of up to 70 % of their own body length, it happens that they choke on the large prey.

1.3.5 Life cycle

Pike spawn one time per year between February and May in the southern part of their distribution and between May and June in the northern part of their distribution. Their life is mostly classified in four stages as follows: embryos (the eggs), larvae (first exogenous

feeding and full development), juveniles (fully developed but not fertile yet) and adults (fertile, mature individuals; Inskip 1982).

Spawning migration

Although pike behaviour during the spawning period has been investigated multiple times and more often in lakes than rivers (Table 1-2), thus far, little is known about the environmental factors influencing migration (Koed et al. 2006, Ovidio & Philippart 2003). It is assumed that migration to spawning grounds is initiated by high flows after ice-out (Craig 1996) and is triggered by an increase of water temperature (Ovidio & Philippart 2003). Nothing is known about the effect of diel temperature change on migration and a potential time lag between migration and water temperature or flow. The relation of migration with temperature and flow during the spawning period is investigated in this study (chapters 3 and 6; Table 1-2). Previous research already indicated that pike may migrate several (7-35 km) kilometres in search for suitable spawning habitat (Koed et al. 2006, Ovidio & Philippart 2003, Pauwels et al. 2014, Vehanen et al. 2006).

Table 1-2: Overview of literature on pike movement and/or migration in lakes and rivers.

Lakes	Rivers
Burkholder and Bernard 1994	Koed et al., 2006
Chapman and Mackay, 1984a and b	Masters et al., 2003
Cook and Bergersen, 1988	Ovidio & Philippart, 2003
Diana, 1980	Vehanen et al., 2006
Jepsen et al., 2001	Pauwels et al., 2014
Kobler et al., 2008a and b	
Lucas 1992	

Reproduction

Previous to mating, the female is mostly accompanied by two smaller males. They swim through and over the vegetation in shallow water and simultaneously spawn eggs and sperm on the vegetation at irregular intervals (Scott & Crossman 1973). Five to six eggs are spawned at a time and this is repeated every few minutes for up to several consecutive hours. Subsequently, the fish rest and restart, potentially with another mate. If environmental conditions are suitable this process continuous till all eggs are spawned. Adults may reside near the spawned eggs for up to two weeks after mating and most adults leave the spawning ground six weeks after mating (Morrow 1980).

In Belgium and the Netherlands pike usually spawns between the beginning of March and the end of April, at water temperatures between 6 and 14°C. Pike spawning preferably occurs on inundated land, where eggs are spawned on grasses (Poaceae), sedges (Cyperaceae), rushes (Juncaceae) and horsetails (Equisetaceae). In the absence of inundated land, pike spawn their eggs on dense emergent vegetation, such as reed sweetgrass (*Glyceria maxima* Hartm.) or bur-reed (*Sparganium*). Previous research indicated that bulrush (*Thypha*) is avoided, probably because this plant grows on H₂S rich bottoms following anoxic conditions (De Laak & van Emmerik 2006). An important aspect is that pike can swim over the vegetation to spawn their eggs. Some authors suggest that depth is influencing the success of spawning more than the type and condition of the vegetation (Craig 1996, Raat 1988b). Pike spawning happens mostly at depths between 25 and 60 cm and seldom at depths greater than 100 cm. Moreover, Inskip (1982) suggests the maximal spawning depth is 50 cm. High wind speed and consequently strong currents, strong water level fluctuations, absence of vegetation and low water temperatures may postpone or even preclude spawning. In that case the eggs are absorbed,

which consequently decreases the fecundity of the female in the next year (Craig 1996, De Laak & van Emmerik 2006). Other variation in the fecundity of the females is subscribed to variations in water temperature, prey availability, social interactions, hydrodynamic aspects and the length and physiologic state of the female (De Laak & van Emmerik 2006).

Development

Also after spawning successful larvae and juvenile development is largely dependent on environmental variables such as vegetation cover, turbidity, pH and oxygen saturation. For instance, the duration of the embryonic development (incubation time) is inversely correlated with water temperature, whereas the survival of the eggs is positively correlated. In Belgium, eggs hatch on average 10 to 13 days after fertilization (Vandelannoote et al. 1998).

Larvae attach themselves to plants after hatching as long as they can live on the yolk. When they have a length of 13 mm on average, they enter the free swimming stadium. Mostly, this is eight to 11 days after hatching (Raaij 1988b). The larvae live near the surface water close to the spawning location and eat zooplankton. By the time they reach the 28-40 mm body length, this is generally 40 days after hatching, they migrate to deeper water with emergent vegetation. In a natural situation this migration is triggered by a decreasing water level (Raaij 1988b). The larvae further develops in the emergent vegetation and at 65 mm length it enters the juvenile stage. Presence of dense emergent vegetation is essential for growing larvae and juveniles to hide from cannibalistic congeners (Holland & Huston 1984).

Between May and June, the further developing juvenile pike (0+ pike) can still be found in sheltered shallow environments, vegetated riparian zones or inundated areas. Depending on the quantity of submersed vegetation in the open water, juveniles will migrate to the open water between June and October. If submerge vegetation and therefore shelter is largely absent, many juveniles will get caught by larger congeners. The survival success of juvenile pike largely depends on prey availability and availability of sheltered, vegetated areas, reducing the degree of cannibalism at high prey and vegetation availability. It is therefore important that water level rises during winter months, thus increasing the availability of inundated vegetated areas, which compensates the loss of emergent and submersed vegetation from autumn onwards. An artificial constant water level, mostly with the intention of preventing inundations, may thus be very detrimental for the successful survival of a pike population (Grimm & Klinge 1996).

Pike may mature after one year at optimal environmental conditions (De Nie 1996), however mostly it is after two to three years and on average at 40 cm body length. Exceptionally, when very few spawning pike occur in the population, pike may mature from 18 cm onwards.

1.3.6 Qualitative environmental relations

The preceding information already indicates that many environmental variables, beside characteristics intrinsic to the population, may positively or negatively influence pike at different life stages. Generally, these variables can be classified as biological environmental variables (emergent and submerge vegetation cover, prey density, predator density, etc.), physical-chemical environmental variables (water temperature, hydrodynamics, O₂ and H₂S concentrations, etc.) and population characteristics (year class strength (YCS), pike density, degree of cannibalism, etc.). We give an overview of these qualitative relations in Figure 1-4. Many thorough practical and empirical studies have been conducted in the past that quantify these relations. An extensive overview of the studies on one or more of the qualitative relations illustrated in Figure 1-4 are listed in Table 1-3.

Table 1-3: Overview of the studies on qualitative environmental relations of pike population dynamics and behaviour (see also Figure 1-4 for an overview of the qualitative environmental relations; YOY: Young-of-the-year pike, YCS(I): year class strength (index), YCF: year class formation).

Environmental variable	Relation:	Reference
Population characteristic/process		
Depth		
	Spawning habitat use	(Farrell et al. 1996)
	Mortality eggs and embryos	(Farrell 2001)
	Pike length and age	(Casselman & Lewis 1996a)
Water temperature		
	Mortality ratio of 20-37 mm pike	(Jacobsen et al. 2007)
	Egg abundance and growth and survival of YOY	(Farrell et al. 2006)
	YCS	(Casselman & Lewis 1996)
	Egg development	(Cooper et al. 2008)
	YCF	(Smith et al. 2007)
Flow velocity		
	Maximal sustainable velocity for adult movement	(De Laak & van Emmerik 2006, Jones et al. 1974)
	Inhibition of spawning migration	(Inskip 1982)
Turbidity		
	Adult movement	(Jepsen et al. 2001)
	Habitat use of 0+ pike	(Skov & Koed 2004)
	Habitat use and feeding behaviour of 0+ pike	(Skov et al. 2002)
	Mortality ratio of 20 mm pike	(Skov et al. 2003a)
	Feeding ratio and intraspecific interference	(Nilsson et al. 2009)
	Feeding and hiding behaviour of pike larvae	(Lehtiniemi et al. 2005)
	Adult movement (57-85 cm)	(Jacobsen et al. 2008)
Vegetation		
	Spawning habitat use	(Farrell et al. 1996)
	Adult pike abundance	(Casselman & Lewis 1996)
	Pike body length	(Casselman & Lewis 1996)
	Anti predator behaviour of pike larvae and juveniles	
	YOY behaviour	(Hawkins et al. 2003)
Salinity		
	Sympatric populations	(Limburg & Westin 2002)
	Mortality ratio of 20-37 mm pike	(Jacobsen et al. 2007)
pH		
	yolk-sac fry	(Keinanen et al. 2000)
Water level		
	Mortality eggs and embryos	(Farrell 2001)
	YCF	(Smith et al. 2007)
Cannibalism		
	Habitat use of 0+ pike	(Skov & Koed 2004)

Feeding success, population dynamics and individual life history	(Claessen et al. 2002)
YCS, population density and individual life history	(Kiplig & Frost 1970, Treasurer et al. 1992)
Growth and body length distribution	(Persson et al. 2006)
Prey heterogeneity	
Mortality ratio of 20 mm pike	(Skov et al. 2003a)
Prey biomass	
Feeding behaviour and habitat use of 0+ pike	(Skov et al. 2002)
Feeding success	(Skov et al. 2003b)
Mortality ratio of 20 mm pike	(Skov et al. 2003a)
Seasonality in feeding behaviour	(Soupir et al. 2000)
Pike behaviour at prey absence	(Venturelli & Tonn 2006)
Mortality and YCS	(Kipling & Frost 1970)
Zooplankton biomass	
Habitat use of 0+ pike	(Skov & Koed 2004)
Zooplankton quality	
Larvae growth	(Engstrom-Ost et al. 2005)
Habitat complexity	
Habitat use of 0+ pike	(Skov & Berg 1999, Skov & Koed 2004)
Mortality ratio of 20 mm pike	(Skov et al. 2003a)
Pike density	
Growth in biomass and population dynamics	(Edeline et al. 2010)
Population growth	(Rose et al. 2001)
General habitat suitability	
Reproduction effort (fecundity, growth, mortality, maturation and biomass of spawning stock)	(Craig & Kipling 1983)
General movement/migration dynamics	
Connectivity between spawning and nursery habitat	(Craig 2008)
Genetic diversity	(Bosworth & Farrell 2006)
YCSI of pike in St Lawrence river	(Farrell et al. 2007)
Nursery behaviour	
Growth, development and survival	(Farrel et al. 2006)

1.4 Pike status in Flanders

Northern pike used to be very common in Europe and North America, but changes in water level, temperature, shoreline development, watershed alterations, siltation, aquatic macrophyte cover and sport fishing beside other factors caused prey fish and pike population declines (Casselman & Lewis 1996). Specifically, in Germany pike is currently classified as a vulnerable species and in Flanders it also suffered significantly from the widespread decrease of water quality and habitat destruction (De Nayer & Belpaire 1997, Goethals et al. 2006, Vandenabeele et al. 1998). In contrast to other European regions, such as Scandinavia, and North America there is no commercial inland fisheries in Belgian waters of significance (www.fao.org). Although we have no data on pike exploitation rates by recreational angling

in this study area, it is not likely that recreational fishing caused the observed population decline from the seventies onwards. Harvest of pike due to recreational fishing and accompanying regulations have not changed substantially through history in Belgium. Population declines were caused by water quality deterioration, habitat destruction and habitat obstruction. Water quality has improved substantially thanks to great efforts since the nineties; however, it is now assessed that the water quality improvement will only further result in enhancement or restoration of fish populations after habitat rehabilitation and defragmentation (Dumortier et al. 2009).

Although historical evidence of a high-density population of pike in our study area exists, densities have been low since the first standardised observations in 1996 (Research Institute for Nature and Forest; INBO; www.vis.inbo.be). This was further evidenced by the large effort needed to catch 15 adult pike at the start of the telemetry study in the river Yser (chapter 3). Fishing campaigns of the INBO (www.vis.milieuinfo.be) between 1998 and 2002 in 9 of the 12 river basins in Flanders revealed a poor status of pike in rivers. In the basin of the river Yser pike was relatively most present, specifically in 21.4 % of the fished locations. The INBO freshwater fish sampling network studies fish at around 900 locations in Flanders. At regular time intervals the fish abundance and species richness is examined and the body length and mass of the caught fish is determined, hence to evaluate potential changes in fish stocks. The sampling locations are carefully selected and distributed over flowing and standing waters and canals and polder watercourses. The type of the sampled water body determines the type of sampling technique, which can be fishing by fyke nets, electricity or trawls.

Although the locations fished in Flanders between 2007 and 2012 covered the Flemish area well, they still only partially indicate the actual pike distribution. Addition of fishermen data and data previous to 1998 could further complete the picture. Further, the distribution of the sampling locations over the different river basins is not homogeneous (Figure 1-5a). Specifically, the basins of the river Lys and the lower river Scheldt are relatively less sampled and the basin of the river Zenne was not sampled between 2007 and 2012 within this freshwater fish sampling network. The river Nete basin was sampled most intensively and the sampled locations are most homogeneously distributed. Fifty of hundred fifty five sampling locations where pike was caught are situated in water bodies where pike was stocked (Figure 1-5b).

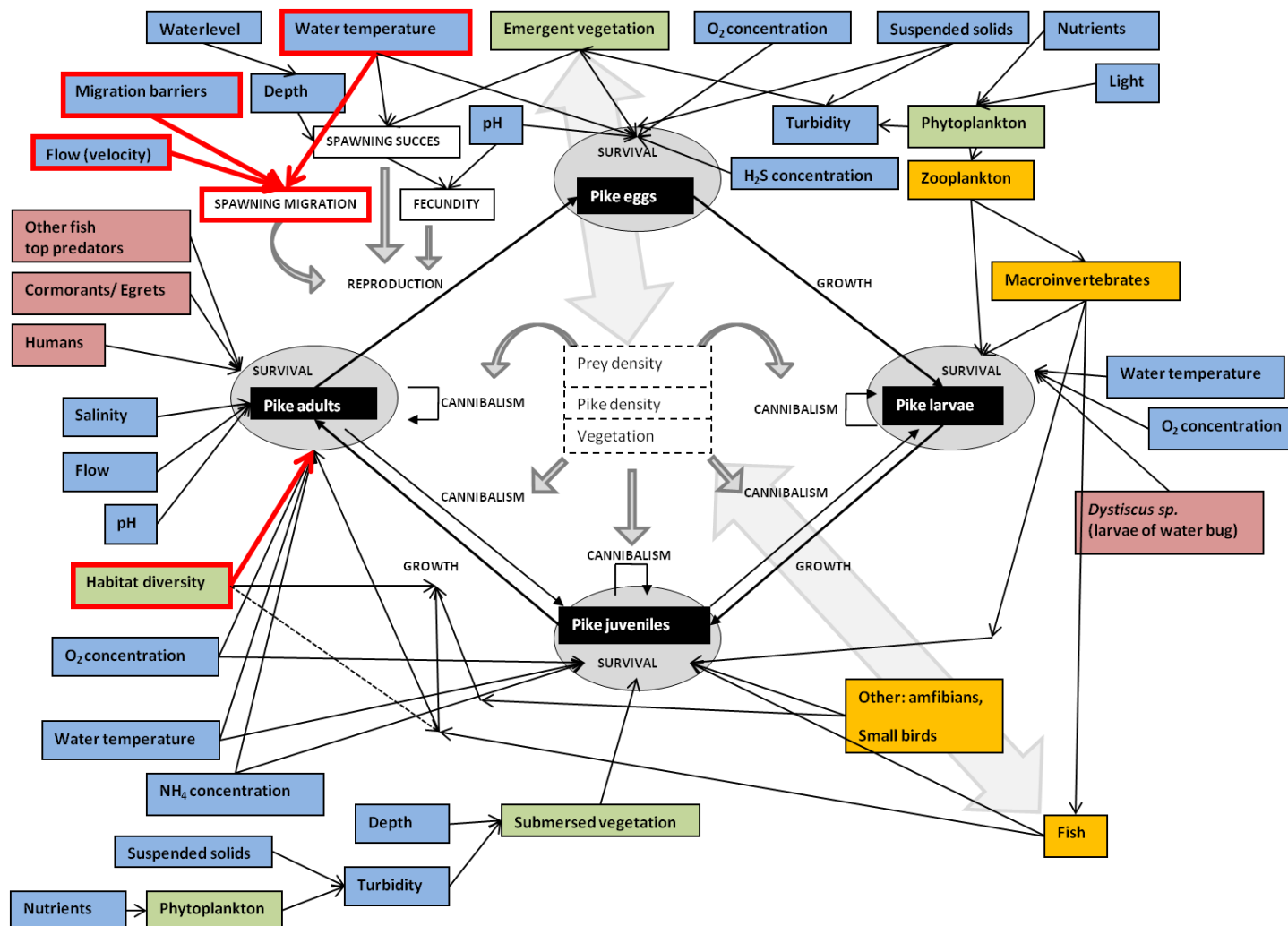


Figure 1-4: Overview of the biological (green: habitat related, yellow: prey related and dark red: predators related) and physical-chemical (blue) environmental variables affecting the life cycle of pike (*Esox lucius* L.). The relations investigated in this thesis are indicated in red.

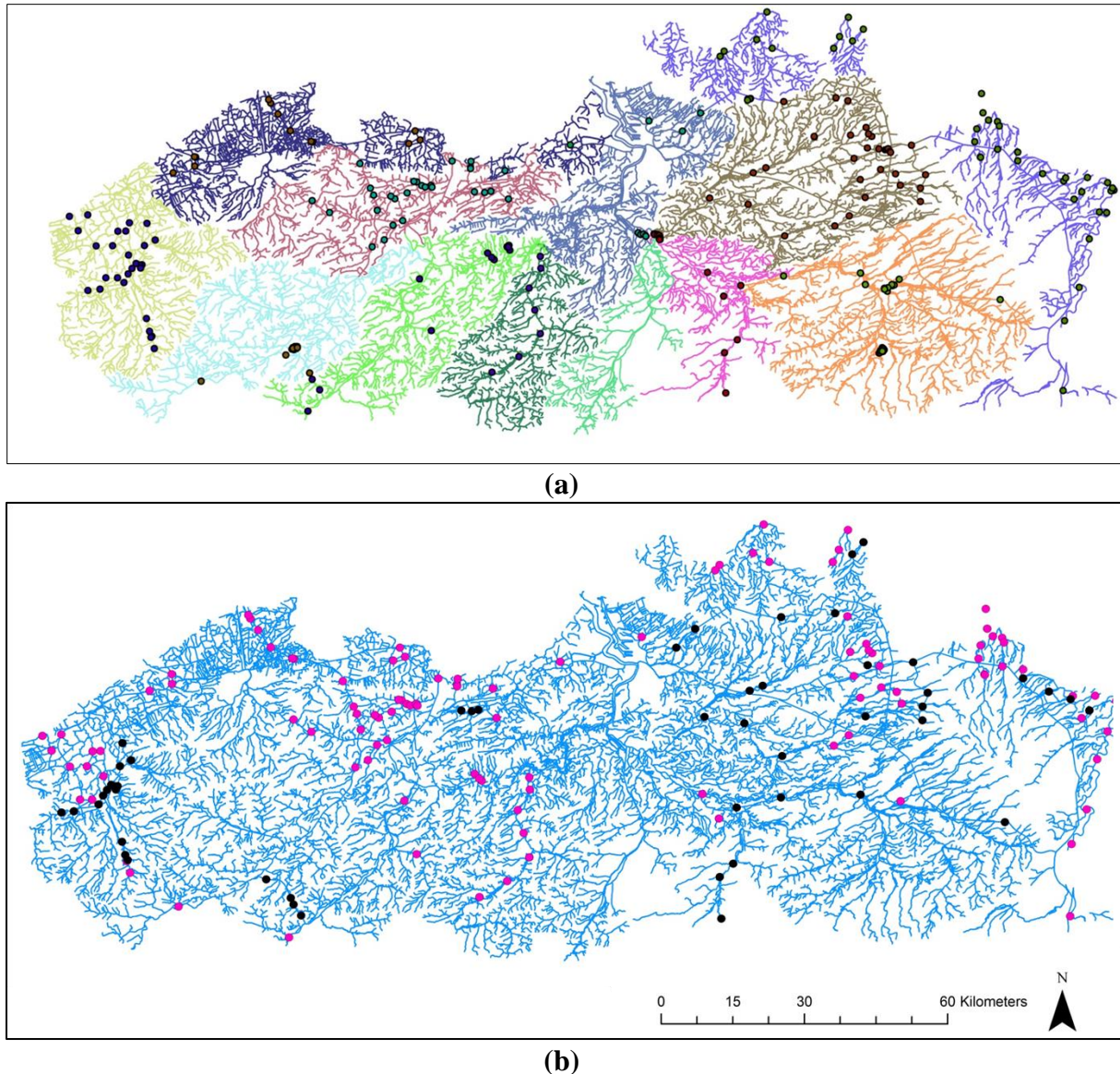


Figure 1-5: a) Distribution of sampling locations of the freshwater fish sampling network (INBO) over twelve river basins in Flanders, Belgium (Left to right bottom: basin of the river Yser, basin of the river Liss, basin of the upper Scheldt, basin of the river Dender, basin of the river Zenne, basin of the river Dijle, basin of the river Demer, basin of the river Maas; left to right top: basin of the polder water courses, basin of the Canals of Ghent, basin of the lower Scheldt, basin of the river Nete). b) Indication of the sampling locations in water courses that are stocked with pike (black dots) and sampling locations in water courses without pike stocking (pink dots).

The fishing protocols adopted in the freshwater fish sampling network ensures uniformity among the samples and aims at collecting numerous qualitative and sporadic quantitative fish data. Different protocols exist per type of water body such that flowing waters are fished with a periodicity of two to three years, except large streams, which are fished every three to four years. Canals are fished every five years, whereas standing water bodies are fished every seven years. Between 2007 and 2012 this resulted in more locations fished by electricity than by fyke nets in all basins. Furthermore, the catch effort by electro-fishing was relatively higher in the basins of the Canals of Ghent, the basin of the river Maas, the basin of the river Yser and the basin of the river Nete (> 40 times each) and the catch effort by fyke nets was relatively higher in the basins of the river Yser and river Dender (between 10 and 20 times

each for the period of 2007-2012). Following these different catch efforts, pike occurrence/biomass is evaluated as the catch per unit effort (CPUE) per basin instead of the total catch per basin. The CPUE is the average abundance (expressed as number or biomass) of fish per catch effort. The catch effort is one fyke sample per 24 h or 100 m of electro-fished river stretch.

Table 1-4: The catch per unit effort (CPUE) and stocking of pike in the twelve river basins for fishing by fyke nets or electro-fishing during the period 2007-2012 (INBO; www.vis.milieuinfo.be; *: highest value, **: second highest value; *: third highest value).**

Basin	CPUE fyke nets (number/24 h)	Total biomass fyke nets (kg)	CPUE electricity (number/100 m)	Total biomass electricity (kg)
Canals of Ghent	0,250	3,400	1,843*	23,731
Polder water courses	0,393	10,838	-	30,048**
Lower Scheldt	0,500***	0,020	2,080***	2,576
River Demer	-	-	-	-
River Dender	0,816*	66,300*	0,342	32,644*
River Dijle	-	-	0,497	18,997
River Liss	-	-	-	-
River Nete	0,250	4,525	1,323	16,218
River Maas	0,175	1,369	2,029**	24,599
River Yser	0,376	21,892***	1,242	28,349***
River Zenne	-	-	-	-
Upper Scheldt	0,600**	22,357**	1,417	15,099

The basins of the polder water courses, the lower Scheldt, the river Maas, the Canals of Ghent, the river Yser and the river Nete had the highest CPUE of electro-fishing (Table 1-4; INBO; www.vis.milieuinfo.be). All contained on average more than 1 pike per 100 m electro-fished river stretch in contrast to the other basins where the CPUE of electro-fishing was lower. The CPUE of fyke nets was highest in the basins of the river Dender, the Upper Scheldt, the lower Scheldt, the polder water courses and the river Yser. However, none of these basins had a CPUE of more than one pike per fyke net per 24 h (Table 1-4; INBO; www.vis.milieuinfo.be).

In an attempt to rehabilitate pike populations, reintroduction programs were started. Specifically, in Flanders between 2003 and 2012 around 300 000 pike eggs, 50 000 larvae, 15 000 juveniles (0 to 3 years old) and 5 adults were released at 10 to 30 different streams per year (Table 1-4). However, these programs are only moderately successful due to the poor water quality, the loss of suitable habitat (Maeckelberghe 2002, Vandenabeele et al. 1998), and the obstruction of fish migration (Verreycken et al. 2012).

1.5 A road map to this thesis

This thesis consists of four main parts of which two parts run in parallel: a modelling part (part II.) and a field-data analysis part (part III.). Both follow from basic information on the studied topic and methodology (part I.) and lead indirectly (modelling) and directly (field-data analysis) to conclusions on pike management (part IV; Figure 1-6).

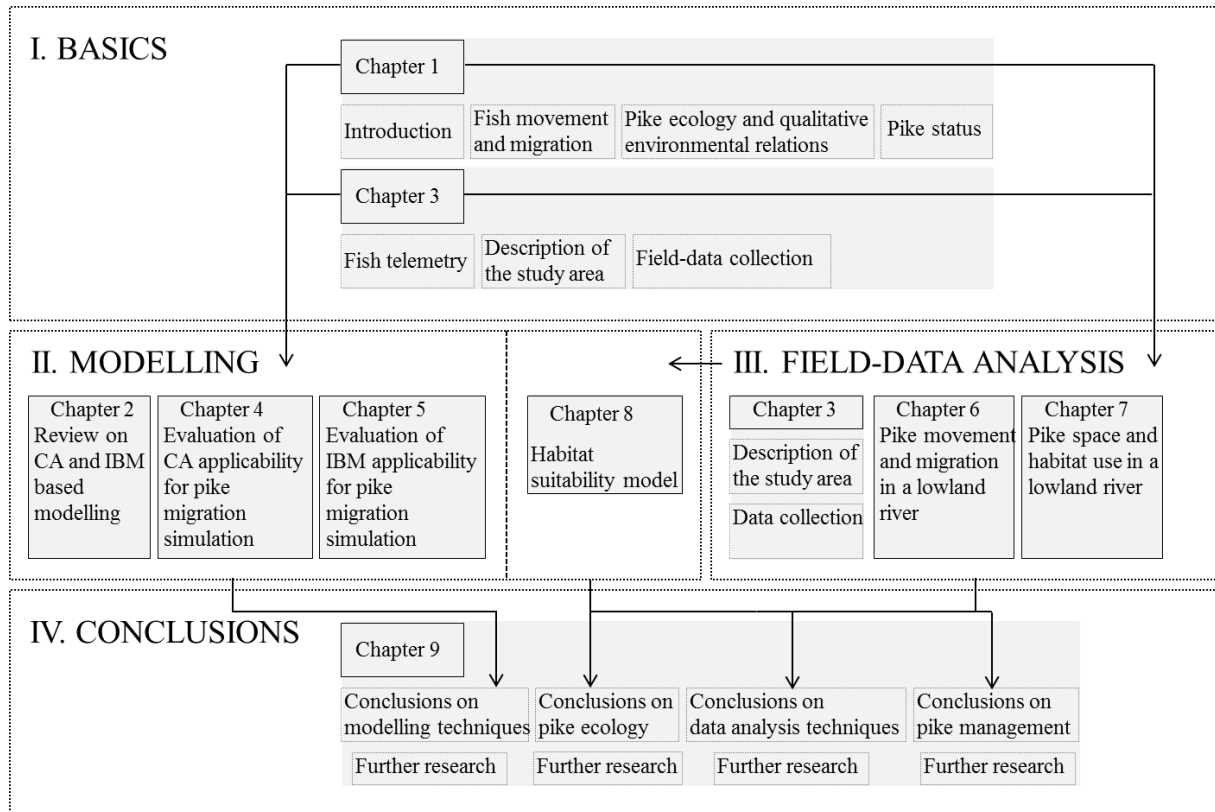


Figure 1-6: A roadmap to this thesis.

In **Chapter 2** firstly the CA and IBM modelling techniques are introduced and their application in modelling species migration is reviewed. Next, the potential opportunities and shortcomings are discussed based on the examples from the past.

In **Chapter 3** firstly the principles of telemetry are introduced and an overview of the current telemetry methods beside radio telemetry is given. Further, the study area, which is the river Yser (Belgium) and the adult and juvenile pike data collection by radio telemetry and electro-fishing, respectively, are described. This information applies on all following chapters, including the chapters on the evaluation of modelling pike migration in a river (chapters 4, 5 and 8) and the development of a habitat suitability model for adult pike in the river Yser (chapter 8; Figure 1-6).

Chapter 4 focuses on the evaluation of the CA modelling paradigm to simulate adult pike migration in a grid that partly represents the river Yser. The CA-based model consists of a grid of cells that have a habitat suitability, which is pragmatically deduced from data on the bank characteristics and knowledge from literature on pike ecology. To evaluate the applicability the sensitivity of the model for the following model parameters was assessed: the number of pike in the grid, the initial pike distribution and the grid resolution was evaluated.

Chapter 5 evaluates the applicability of the IBM modelling technique to simulate adult pike migration in a part of the river Yser. This IBM takes inspiration from the one developed to simulate the formation of fish schools, extended so that (1) the IBM is adapted to mimic the dynamics of a solitary fish species, (2) it is calibrated by means of collected pike trajectory data, and (3) the model has a realistic initial condition.

In **Chapter 6** the results on the analysis of the movement and migration dynamics of adult pike in the river Yser are described and discussed. Specifically the analysis focuses on the relation of movement and migration with environmental variables, such as water temperature and flow.

Chapter 7 describes and discusses the results on the analysis of the habitat use and habitat preference of adult pike in the river Yser. The habitat use and preference are analysed at two spatial scales: the macro- and meso-scale. At the macro-scale the use of the following river parts is assessed: the main river, the large and small tributaries and the natural and artificial side arms. At the meso-scale the use of and preference for the eight riparian habitat types of the study area are evaluated. These riparian habitats are a combination of three vegetation types (reedy, woody and no vegetation) and three river bank types (artificial vertical banks, semi-natural banks and artificial foreshores). The analysis accounts for differences in habitat availability between individuals by determining the use and preference at three orders of habitat selection that differ in the definition of used (home ranges or pike observations) and available habitat (whole study area or pike's home range).

In **Chapter 8** the field-data on the river Yser and on the adult pike, and knowledge on adult pike ecology are integrated in a habitat suitability model. Model development is based on crisp sets defined by expert knowledge, and the sets were used to derive "if-then knowledge rules" from the field-data set. The sensitivity of the model performance to each input variable is evaluated to get insight in the importance for the variables in predicting pike habitat suitability. Further, the resulting rule base is analysed and compared to the results from the field-data analysis on habitat use and preference of adult pike.

The main conclusions on this PhD research are described in **Chapter 9**. The applicability, shortcomings and further research on the CA and IBM modelling techniques for simulating pike migration in a river are discussed based on the results of chapters 2, 4, 5 and 8. New conclusions on pike behaviour following from the analyses described in chapters 3, 6 and 7 are described and advice on river management is given based on the results and conclusions of the modelling chapters and the results and discussion on the field-data analyses.

CHAPTER 2

Modelling fish migration

2.1 Introduction

Past decades, loss of natural habitat by canalization, dam construction, water pollution, eutrophication and overfishing caused substantial fish population declines. Specifically, migratory fish suffer from habitat fragmentation because the habitats they need to rest, hide, forage and reproduce are typically dispersed and thus entail frequent small scale movements and sporadic large migration events (Lucas et al. 2001, Northcote 1978). Hence, it is evident that obstruction of these movement and migration events by dams, sluices and other water technical constructions strongly hamper their successful reproduction. Consequently, one of the major challenges facing river scientists and managers the past years is efficiently allocating river rehabilitation efforts, such as creation and rehabilitation of fish passages, natural banks and floodplains or spawning grounds. Therefore information on the habitat requirements and spatial dynamics of the fish species is crucial, as well as the specific habitat requirements of each species, the distribution of suitable habitats and the quality of the intermediate river stretch. To gain insight into these aspects many models are developed over the course of several years. We give here only the most recent ones out of a tremendous number of examples (Costa et al. 2012, Dunbar et al. 2012, Ziv et al. 2012, Zorn et al. 2012). Some of the models concentrated on simulating abundances or population growth rates (Arlinghaus et al. 2010, Catalano & Allen 2010, Kerr et al. 2010), others specifically modelled gene flow (Dillane et al. 2008, Gomeziuchida 2009), still others explicitly linked habitat supply to fish population dynamics (Guay et al. 2000, Vilizzi et al. 2004) and some modelled the distribution of species based on this habitat supply (Williams et al. 1999). These modelling techniques are helpful tools in understanding the suitability of local, critical habitat variables such as water depth, flow velocity and vegetation characteristics. However, they do not allow to model population viability constraints by wider, large scale variables, such as migratory access (Mcdowall 1993). Since it is likely that this variable constrains the abundance of migratory species more than local habitat variables, habitat suitability and

population growth models for migratory fish should take into account factors relating to migration and accessibility (Hayes et al. 2009).

Consequently, modelling techniques (further called spatially explicit and dynamic modelling techniques) should be exploited that allow accounting for spatial and temporal heterogeneity, beside processes of migration. Promising techniques in this respect are individual-based modelling (IBM) or similarly group based modelling (GBM) and the cellular automaton modelling paradigm (CAs).

The goal of this chapter is to review the application of spatially explicit and dynamic modelling techniques such as IBMs and CAs, to model stream fish and specifically to simulate fish migration. Our intent is not to provide a complete list of all the studies that ever applied the IBM or CA modelling paradigm in this context, but rather to give an idea on their applicability to model migratory fish, by assessing the methods used and major challenges and opportunities encountered. In the light of this discussion, we identify desirable features for migration simulating spatially explicit models aimed at policy evaluation, and particularly Northern pike (*Esox lucius*) management evaluation. In contrast to other migratory fish, such as several species of salmonids (*Salmonidae*; Frank et al. 2001) pike was not often modelled yet using the IBM technique and pike migration was not modelled using the IBM and CA modelling paradigm. This is more or less surprising since many pike populations, specifically in lowland rivers, face the same viability decreases due to habitat degradation and fragmentation.

2.2 Spatially explicit modelling

2.2.1 Eligible modelling techniques

Although species distribution models may reveal new insights into the ecology of fish and their functioning within ecosystems (Glasbergen 2001, Guisan & Zimmermann 2000, Inskip 1982, Kerle et al. 2001, Mouton 2008), they are often limited to either temporal or spatial fluctuations in fish distribution. Consequently they do not provide information on the spatial dynamics of fish, although many fish species typically need different, spatially separated habitats to successfully complete their life cycle.

Present day mathematics provides modellers with a wide range of mathematical constructs (throughout this thesis named modelling techniques) that can be exploited to describe environmental processes that are spatially heterogeneous and dynamic. These modelling techniques are conveniently classified based on the structure of the involved region in space-time and the nature of their state space (Baetens 2012). Both space and time can be considered as a continuum or a composition of discrete entities (Berec 2002). Furthermore, also state space of each model can be continuous, if the value of the dependent variable can be anything out of an infinite number of possibilities, or discrete, if there exists only a finite number of possible states. Considering that each model is characterised by one space-time region and one state region, eight types of modelling techniques can be defined (Table 2-1).

Table 2-1: Classification of spatial-temporal models according to the characterisation of their space-time region and state space (C = continuous; D = discrete; Baetens 2012).

Time	Space	State	Common label	Constructs ¹
C	C	C	PDE-based model	PDEs
C	D	C	Spatially implicit model	ODEs
D	C	C	Reaction-diffusion models	IdEs
D	D	C	Coupled-map lattice	PdEs
C	C	D	Spatial point model	Set of rules
D	C	D	Individual ² -based model	Set of rules
C	D	D	Interacting particle system	Set of rules
D	D	D	Cellular automaton	Set of rules

¹ IdE: Integro-difference Equation; ODE: Ordinary Differential Equation, PDE: Partial Differential Equation, PdEs: Partial difference Equations

² Individual or agent-based model

To enable the spatially explicit and dynamic modelling of migratory species, Geographical Information Systems (GIS) and the mathematical paradigms of partial differential equations (PDEs), individual-based models (IBMs) and cellular automata (CAs) were introduced in ecological modelling. Recently, (Chen et al. 2011) reviewed these modelling paradigms, their usability and shortcomings. They point out that, although GIS and remote sensing are powerful tools for spatial analysis, these give an inherently static view of the world and are unable to capture and model dynamic processes. PDEs can describe the abundance of a species both spatially and temporally, but neglect spatial heterogeneity, local interactions and individual differences, since they rely on mean-field assumptions (Chen & Mynett 2006). In contrast, IBMs allow to model the dynamics of individuals in an ecosystem that shows non-uniform variation of environmental variables (Perry & Enright 2007), and therefore have been applied frequently in this context (Le Fur & Simon 2009, Li et al. 2010, Uchmanski et al. 1999, Yemane et al. 2009). CA models are similar to IBMs but focus on the effect of spatially and temporally heterogeneous environmental conditions on the population, rather than on the individual characteristics and behaviour. In the following sections the conceptual aspects of IBMs and CAs are depicted.

2.2.2 Conceptual aspects on IBMs

Past two decades there has been an enormous growth in individual-based modelling in ecology and evolutionary biology. Concurrently, several good reviews have been written on IBMs studying this modelling technique from different points of view. Three of the most recent reviews that are most comprehensive are highlighted here: Berec 2002, DeAngelis & Mooij 2005 and Grimm & Railsback 2005. However, many more reviews exist (Huston et al. 1988, Hogeweg & Hesper 1990, Judson 1994, Uchmanski et al. 1999), beside the ones that focus on subfields of ecology, such as Berger & Rivera-Monroy (2008), who review advances and limitations of IBM application in mangrove forest modelling, Matthews et al. (2007), who describe the application of agent-based models in land use modelling and Winkle (1993) who gives an overview of individual-based approach to fish population modelling. Of the three most recent comprehensive reviews on IBMs, Berec (2002) is the one giving a state-of-the-art technical overview of spatially explicit IBMs. He provides and relates four different frameworks in which spatially explicit IBMs can be defined. DeAngelis & Mooij (2005) described IBMs according to 5 major types of individual variation: spatial, ontogenetic, phenotypic, cognitive and genetic, and they considered the application of IBMs in several subfields of ecology, of which fish recruitment is one. In contrast to Grimm & Railsback (2005), their objective was more investigative and they based their review on 900 references

to find out the field of IBM had developed over the preceding years. Grimm & Railsback (2005) provided an extensive description of IBMs in the light of the usefulness of IBMs to determine the interrelationship between individual traits and system dynamics. Their work was reviewed as a well-written book about the theory, framework, practical steps and applications, as well as possibilities for future developments in the area of IBMs (Stadtländer 2012). The majority of concepts and technical aspects on IBMs described below are based on these manuscripts.

What is an IBM? DeAngelis & Mooij (2005), as well as Grimm et al. (2005) state that no absolute definition exists. In principle, IBMs simulate populations or systems of populations as being composed of discrete agents that represent individual organisms or groups of similar individual organisms, with sets of traits that vary among the agents. Each agent has a unique history of interactions with his environment and other agents. IBMs attempt to capture the variation among individuals that is relevant to the questions being addressed (DeAngelis & Mooij 2005). The essence of the IBM approach is to derive the properties of ecological systems from the properties of the individuals constituting these systems (Lomnicki 1992), hence following the belief that one must zoom down to the lower level of the individual to understand population and community phenomena (DeAngelis & Mooij 2005).

Essentially, the basic structure of IBMs is a collection of discrete individuals. Discreteness and adaptive behaviour of these individuals is considered essential in IBMs. The discrete individuals can be true individual organisms or a homogenous group of individuals considered as one unit. Besides, IBMs consist of state variables, which describe the state of the system; essential processes, which cause changes of the state variables and parameters, which are used in the sub-models of the essential processes. These are moreover equations and rules that quantify when, how much and how fast the variables change and hence define the model's dynamics (Grimm & Railsback 2005). Consequently, for every IBM development, variables have to be selected describing the state of the individuals, parameters describing the individuals' behaviour and variables and parameters describing the individuals' environment with which they interact (Grimm & Railsback 2005). Although many models that meet this definition are published as IBMs, they are not necessarily so according to Grimm & Railsback (2005). These authors describe four criteria that indicate what makes a model a true IBM. (1) The first one is the degree to which complexity of the individual's life cycle is reflected. (2) The second criterion is whether or not the dynamics of resources used by individuals are explicitly represented. (3) Further, whether real or integer numbers are used to represent the size of a population is a good indicator. (4) Finally, the extent to which variability among individuals of the same age is considered defines whether a model is a true IBM or not. Based on these criteria, Grimm & Railsback (Grimm & Railsback 2005) state that IBMs ... :

1. have to consider growth and development of the individuals in some way, otherwise they neglect essential aspects of the "ecology of individuals" (Uchmanski et al. 1999);
2. should account for, often local, feedback between individuals and resources and therefore cannot assume a constant carrying capacity for resources;
3. are built using the mathematics of discrete events, not rates, so population sizes are integers, since individuals are discrete;
4. account for variation among individuals within the same class (e.g. size class or age class).

Besides, Grimm et al. (2006, 2010) proposed a protocol for the proper description of IBMs in publications to enhance reproducibility of each model. This protocol is called the ODD protocol, which refers to Overview, Design concepts and Details. The basic idea of the protocol is to always structure the information about an IBM according to these three parts, which are further subdivided in different elements. Specifically, to give a good overview of

the developed IBM one should first describe the purpose, then the state variables and scales, and lastly an overview of the processes and scheduling (Grimm et al. 2006). Good examples of state variables are age, sex or length or social rank of individuals. These are variables that characterise the basic elements of the model: the individuals. The processes can be environmental as well as individual processes, such as food production, feeding, growth and movement. A description of the design concepts should serve as a framework for designing and communicating the IBMs and may entail an explanation of, among others, the potential inclusion of stochasticity in the model, the inclusion of interactions between individuals or the incorporation of conclusives such as families or age classes. Finally, details should be given on the initialization of the model, the input and the submodels used in the IBM (Grimm et al. 2006). Hereby, the initialization clarifies for instance how individuals and the environment are created at the start of a simulation run, or what the initial values of the state variables are. The input of the model refers to the dynamics that are imposed on certain state variables, such as environmental variables that change through time. All the environmental variables that are taken into account, together with their initial values are defined as the input of the model. The submodels are the models simulating the processes that are listed under “processes and scheduling” (Grimm et al. 2006).

Compared to most of the modelling techniques, IBMs entail a distinctly different way of thinking about ecology. In contrast to classical theoretical ecology, which usually ignores individuals and their adaptive behaviour, IBMs view higher organisational levels (populations, communities, ecosystems) as complex systems with properties that arise from the traits and interactions of their lower-level components: the individuals (Grimm et al. 1999, Grimm & Railsback 2005). As proposed by DeAngelis & Mooij (2005), zooming in to the resolution of the individual can be categorized as an increasing level of mechanistic detail along each of five directions of axes. The structural characteristics along these axes are (a) spatial variability, local interactions and movement; (b) life cycles and ontogenetic development; (c) phenotypic variability, plasticity and behaviour; (d) differences in experience and learning; and (e) genetic variability and evolution (DeAngelis & Mooij 2005). The axis that is important for the models applied in this dissertation is (a), since the individual characteristics modelled relate to movement. The review of IBMs developed and applied on migratory fish here will therefore concentrate on this axis.

2.2.3 Conceptual aspects on CAs

The primitive concepts of CAs date back to the late 1940s, but during their following existence, CA models and applications have been created, developed and used in many different fields (Bandini et al. 2001). The conception of CAs is based on the original idea of John von Neumann (1966). Shortly after, Thatcher (1964), Codd (1968) and Burks (1970) contributed to completing and improving the model. An important work on CA as dynamical systems was done by Wolfram (1986, 1994), with the interpretation of the 1 dimensional CA dynamics in the framework of statistical physics. Following these publications, the interest in CA grew in different directions, and they were studied from different perspectives and applied in different research fields (Bandini et al. 2001).

Some of the research fields in which the application of CAs was first successful is in modelling fluid dynamics, in which a case of an industrial CA was the simulation of water percolating processes, such as water through the soil (Bandini et al. 2000, Bandini et al. 2001). Biology is one of the first disciplines involved in the application of CA and as Bandini et al. (2001) indicate, there are generally two branches in the biological CA applications. The first falls in the topic of Artificial Life models, whereas the second regards modelling, but also studying dynamical properties of biological phenomena. Most of these phenomena are rather static organisms instead of migrating animals. As such, CAs have been applied to

simulate vegetal growth, such as simulations of macrophytes dynamics, harmful algal blooms (Mynett & Chen 2004) and investigations of the response of the boreal tree line to environmental forcing factors, among others (Baltzer et al. 1998). These are nice examples of applications of CA in conservation biology and environmental management. Other examples in this respect are the application of simulating the spread and evaluating the eradication of invasive species, and simulations of water quality to determine cause-effect relations between sources of pollution and the observed quality of the water. Besides, CA have been applied for risk assessment by combination with GIS to simulate forest fire spread (Tao et al. 2013), describe seismicity (Jimenez 2013) and evaluate the spread of diseases (Fresnadillo Martinez et al. 2013). Although many more examples exist, one last biological research topic to mention is simulations in predator-prey interactions (Ferrerri & Venturino 2013). Beside biological applications, CA have been applied multiple times in urban planning (Barredo et al. 2003, Chen et al. 2014, Moghadam & Helbich 2013, Xie et al. 2010, Xu et al. 2006), and to simulate traffic, for instance in planning traffic lights (Perez-Ocon et al. 2013, Zeng et al. 2014). In spite of the large amount of work made throughout the fields mentioned here and other fields, we gave here only a brief overview.

What is a CA? As proposed by Wolfram (1983) in the most cited (> 1000 cites) definition of a CA:

“Cellular automata are simple mathematical idealizations of natural systems. They consist of a lattice of discrete identical sites, each site taking on a finite set of, say, integer values. The values of the sites evolve in discrete time steps according to deterministic rules that specify the value of each site in terms of the values of neighboring sites.”

Specifically, each CA (ζ) can be represented by the following five elements (Baetens 2012):

$$\zeta = \langle \tau, S, s, N, \Phi \rangle$$

Where (1) τ is a countable infinite tessellation of an n -dimensional Euclidean space \mathbb{R}^n , consisting of cells c_i , $i \in \mathbb{N}$; (2) S is a finite set of k states and is often $\subset \mathbb{N}$; (3) the output function $s: \tau \times \mathbb{N} \rightarrow S$ yields the state value of c_i at the t^{th} discrete time step $S(c_i, t)$; (4) the neighborhood function $N: \tau \rightarrow \bigcup_{p=1}^{\infty} \tau^p$ maps every cell c_i to a finite sequence $N(c_i) = (c_{i_j})_{j=1}^{|N(c_i)|}$, consisting of $|N(c_i)|$ distinct cells c_{i_j} and (5) $\Phi = (\phi_i)_{i \in \mathbb{N}}$ is a family of functions $\phi: S^{|N(c_i)|} \rightarrow S$, each ϕ_i governing the dynamics of c_i . The latter is $S(c_i, t+1) = \phi_i(\tilde{S}(N(c_i), t))$, where $\tilde{S}(N(c_i), t) = (S(c_{i_j}, t))_{j=1}^{|N(c_i)|}$.

According to this definition, $N(c_i)$ constitutes an ordered list of cells, $(c_{i_j})_{j=1}^{|N(c_i)|}$, so in the most general case ϕ_i depends on the ordering of the sequence $\tilde{S}(N(c_i), t)$. However, also order-invariant CAs exist (Baetens 2012).

Characteristic of CAs is the discrete nature of the time, space and state domains (Wolfram 1983, 1998, 2002; Table 2-1). The tessellation (τ) can be composed of regularly or irregularly shaped cells and can be one- two- or three-dimensional. The shape of the cells in regular tessellations can be square, rectangular, triangular or hexagonal. The neighbouring cells affecting the cell state in a next time step are defined by the neighbourhood scheme in square or rectangular tessellations. Two neighbourhood (N) schemes are commonly used if square cells are at stake, namely the Von Neumann neighbourhood scheme, taking into account the state of the cells that share an edge with the cell under consideration, and a Moore neighbourhood that also includes these cells that merely share a vertex (Figure 2-1).

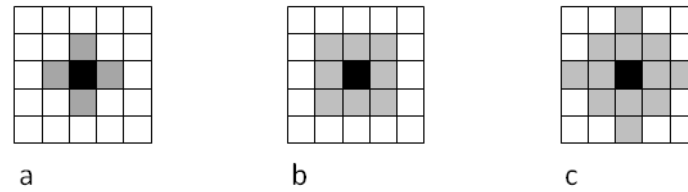


Figure 2-1: von Neumann neighbourhood for range 1 (a), Moore neighbourhood for range 1 (b) and von Neumann neighbourhood for range 2 (c).

In general it is possible to distinguish two main approaches in the creation of CA models: forward and backward (Wolfram 1986). The forward (theoretical) approach concerns the study of transition rules of a given cellular space in order to establish its intrinsic properties (dynamic behaviour, patterns, growth, etc.). The backward (practical) approach regards the design of transition rules sets of a designed cellular space in order to match the “right” behaviour of the CA system of a given complex system (physical, biological, social, urban and so on; Bandini et al. 2001). It is the last approach that is further applied in this thesis and reviewed below.

Li (2009) distinguished four types of CAs, depending on the type of transition rules (Φ) and the ordering of applying Φ . Traditional CAs consist of simple if-then transition rules that are simultaneously applied on all cells. Stochastic CAs deviate from these by the addition of a stochastic component to the transitions rules. Self-learning CAs consist of transition rules that are derived from data using data-driven modelling techniques. In contrast, the transition rules of fuzzy rule-based CAs models are derived from a combination of data and expert knowledge. Depending on the type of CA cells are not necessarily updated simultaneously (Ilachinski 2001).

Table 2-2: Overview of the major types of discrete CA (adapted from Li 2009).

Type of CA	Update of the cell state	Type of transition rules
Traditional CA	Simultaneously	Simple if-then rules
Stochastic CA	Simultaneously or asynchronously	Stochastic transition rules
Self-learning CA	Simultaneously or asynchronously	Internally developed transition rules using data-driven techniques.
Fuzzy-rule based CA	Simultaneously or asynchronously	Fuzzy inference rules

2.3 IBMs in fish migration modelling

IBMs have become very popular over the past decades and have been applied to many migrating animals, particularly fish (Bauer & Klaassen 2013). Their success in modelling migratory species was facilitated by the fast advancement of computer technology (especially object-oriented programming and parallel computing), the increasing availability of spatially resolved data and individual tracking instruments, such as acoustic Passive Integrated Transponder (PIT)-tags, Global Positioning System (GPS) fish tags and radio tags; see chapter 3; Chen et al. 2011, Watkins and Rose 2013). The number of examples of IBMs on fish is tremendous and examples range from simulating the population dynamics (Charles et al. 2008, Clark & Rose 1997b), for instance to quantify effects of intraspecific competition (Clark & Rose 1997a), to evaluating the design and effectiveness of fish passage facilities

(Weber et al. 2006), simulating school fish migration (Hubbard et al. 2004), predicting the effect on populations of fisheries (O'Callaghan & Gordon 2008), spatial arrangement of the environment (Campbell et al. 2011) and protected areas (Moustakas & Silvert 2011, Yemane et al. 2008) and 3D-reactions to abiotic stimuli (Goodwin et al. 2006), among many others.

When first introduced, IBMs of fish (generally animal) behaviour were comparatively rarely used as predictive models, but rather as theoretical models in ecology (Camazine et al. 2003, Willis 2011). However, seen the high pressure on the aquatic environment through human activities such as bank reinforcement, offshore wind farms, coastal squeeze, water level control, climate change and water pollution it became necessary to predict the response of aquatic animals to environmental changes and gain information on their distribution over suitable habitats (Willis 2011). Further, early IBMs generally did not consider the effect of a spatially variable physical environment. However, advances in ocean circulation models from the late eighties onwards, which included realistic temporal and spatial variation in currents, turbulence, light, prey, etc. have enabled IBMs to explicitly consider a realistic spatial heterogenic environment. This provided an additional factor that contributed to the differentiation among individuals, variances in population structure and ultimately understanding of the processes such as birth and growth, and movement and migration (Werner et al. 2001).

Throughout the published fish IBMs, a number of different approaches have been developed to represent the behavioural movement. The approaches make different assumptions about how individuals move in their environment, perceive their environment and respond to it, and use different mathematics to predict the movement responses. Watkins and Rose (2013) described and reviewed these approaches. Restricted-area search assumes individuals are able to evaluate all cells within a defined area and identify the cells with the highest quality habitat (Giske et al. 2003, Haas et al. 2004, Railsback et al. 1999). Artificial neural networks use information about the current location, past experience and other cues to determine directional velocities (Huse & Ellingsen 2008, Huse & Giske 1998). Run and tumble divides the movement into running, where individuals move in a constant direction, and tumbling, where individuals randomly select a new swimming direction (Humphries et al. 2010). Random walk is a common approach where a random turning angle and swimming speed are selected at each time step from defined probability distributions. Random walks can direct movement without considering environmental cues or they can adjust behaviour (angle and speed) based on local information (Codling et al. 2008, Watkins & Rose 2013). In chapter 5 of this thesis we developed a preliminary IBM for Northern pike in which the approach of the random walk and area search are combined, such that depending on the period of the year one or the other approach is applied more intensively.

Most stream fish (diadromous and potadromous) IBMs have been developed for salmonids, such as brown trout *Salmo trutta* L. (Frank et al. 2011, Harvey & Railsback 2009) and Atlantic salmon *Salmo salar* L. (Harvey & Railsback 2009, Hedger et al. 2013, Petersen & DeAngelis 2000, Railsback & Harvey 2002, Smith et al. 2009). The goal of these models differed from modelling habitat selection, to growth rates, over migration, predator-prey interactions, the effect of habitat fragmentation on population persistence, the effect of turbidity on feeding and life-history strategies. Few of these IBMs are spatially explicit (Hedger et al. 2013). Besides, IBMs have been developed for bullhead *Cottus gobio* L. (Charles et al. 2008), European eel *Anguilla anguilla* L. (Melia et al. 2013, Tyler & Rose 1997), Humpback chub *Gila cypha* Miller (Pine et al. 2013) and gudgeon *Hypseleotris spp.* (Perry & Bond 2009), and for marine species, such as anchovy *Engraulis japonicus* (Wang et al. 2013), Lesser sandeel *Ammodytes tobianus* L. (Gurkan et al. 2013, Gurkan et al. 2012) and Arctic cod *Boreogadis saida* Lepechin, among others.

Farrell et al. (2006) developed an IBM on the early life history of Northern pike. The model used temperature as a driving force to predict the timing and location of spawning through egg abundance, stage-specific development, growth, survival and ultimately relative production of YOY northern pike within 1-ha plots in the St. Lawrence River (Canada, USA). This IBM did not simulate migration. No IBM on pike migration has been developed yet.

2.4 CAs in fish migration modelling

In contrast to IBMs and despite the large amount of applications in many research fields, CAs and CA-based models have not often been applied to model fish migration. This is rather surprising seen their ability to simulate complex dynamical behaviours based on a simple definition of local rules. A potential reason is the difficult identification of correct rules for iterating from one time step to the next (Moustakas & Silvert 2011). Furthermore, omission or misinterpretation of significant biological characteristics, or erroneous spatio-temporal ordering of events might lead to trivial results (Ruxton & Saravia 1998).

The applications of CA to fish migration are restricted to the simulation of fish schools of marine fish. One CA was developed to model school formation in tuna *Thunnus thynnus* L. (Stocker 1999), whereas another was used to identify fish dense areas in enhancing clever fishing (Eide 2011). The former is an individual based CA with a hexagonal grid, which has two states: one fish or no fish, and in which the states are updated based on information on the energetic advances for an individual fish based on tail strokes of neighbouring fish, and information on the oxygen concentration in each cell. The latter simulates fish migration in a grid with square cells based on 12 simple rules (one rule per month) that indicate the redistribution of fish biomass over neighbouring cells. The rules were based on knowledge on seasonal variations in catch ability of the Northeast Arctic Cod stock (Eide 2011). A third and last example of the application of a true CA to simulate fish migration, was developed by Vabo and Nottestad (1997) to visualize internal school dynamics based on individual decision rules. The rules of the CA are applied on individual fish as in the CA developed by Stocker (1999), and are based on several anti-predator strategies, such as split, join and vacuole. The model was applied on Norwegian spring-spawning herring *Clupea harengus* L..

Other spatial-explicit and dynamic models on fish migration exist of which it is not clear from the publication whether they are truly CA-based, because it is not clearly described which cells are accounted for in the update of the cell states. One of these models was developed to simulate fish migration in the Eastern Bering sea (Pola 1985), whereas two others were used to evaluate the efficacy of marine protected areas for fish stocks (Moustakas & Silvert 2011, Stefansson & Rosenberg 2006).

2.5 Models on Northern pike *Esox lucius* L.

No IBM or CA has been developed yet that simulates pike migration. However, other models have been developed for pike, of which some are spatial-explicit and others are temporally dynamic. We give a brief overview. The first pike model was developed by Minns et al. (1996) to simulate the impact of habitat supply limits on Northern pike. The model had submodels for spawning, fry, juveniles and 1+ adults. The key population processes in each life stage were controlled by a saturation function on habitat supply. Their research revealed that fry and juvenile-adult habitats in lake Ontario were more limiting than spawning habitat. The next to develop a model on Northern pike were Farrel et al. (2006), who simulated the effects of water temperature on survival, growth and production of juvenile pike in the St Lawrence River based on an IBM on the early life history of Northern pike. The model was based on knowledge on three different spawning patterns, which resulted from empirical studies and a model simulating water temperature, which was developed based on a long

series of water temperature data. One year later two spatially explicit pike models were published. One study investigated the effect of dispersal barriers on the upstream migration of pike in a network of connected lakes using GIS tools (Spens et al. 2007), whereas Mingelbier et al. (2008) developed a model to predict the habitat available for egg deposition and the early stage mortality by dewatering in the St. Lawrence river. The model of Mingelbier et al. (2008) integrated high resolution spatial data on flow velocity, wetland type and water temperature in a habitat suitability index, weighted according to literature. Lastly, Arlinghaus et al. (2009, 2010) presented an ecologically realistic age-structured model specifically tailored to recreational fishing that allows estimating selection differentials on adaptive life-history traits. The model accounts for multiple ecological feedbacks, which result in density-dependent and frequency-dependent selection. None of these models were relied upon for the research described here, since no population growth model was developed. However, the integration in a spatial explicit model of the model of Arlinghaus et al. (2009, 2010) could be of great added value. The model presented by Spens et al. (2007) was not included in this research because it takes river slope as a key variable, whereas the effect of river slope in this study area is expected to be minimal.

2.6 Challenges and opportunities

An ecological model is a set of assumptions about an ecological system expressed in mathematical language. Mathematical reasoning or computation may then be used to generate predictions about the system (Chen et al. 2011, Gurney & Nisbet 1998). Some ecological models make few assumptions and are consequently very detailed, complex and/or restricted to only a small subset of the many processes that may be happening in the studied ecological system, whereas others are based on many assumptions, simulate a system on a broader scale and are therefore less complex and more transparent, but may also be less accurate.

In the previous sections we zoomed in on the multiple spatially explicit ecological models that have been developed to assess (and sometimes predict) the effects on fish populations of environmental changes following from human activities such as fishing, dewatering of areas and obstruction of the migration network, among others. Few of these models were applied on Northern pike. Moreover, the models applied on pike concentrated on pike population dynamics, in some cases related to a heterogeneous environment. None of the models on pike simulated pike movement and migration. From the models that did simulate fish migration, most were applied on individual fish and only a few simulate at the level of the population. Those models who did were restricted to assessing and predicting the effect of fishing and protection from fishing on fish schools.

Irrespective of the difference in the studied scientific problem, the reviewed spatially explicit models differed in the degree to which assumptions are made about the studied system. Generally, the IBMs involved fewer assumptions on the studied system and processes making them more accurate, but also more complex, less transparent and restricted to a subset of processes, whereas the CAs involved much more assumptions on the interaction between the population and the environment, were less complex and transparent but potentially less accurate when used for making predictions.

The challenge of every spatially explicit model that is eventually developed to give management support is to accurately model and predict a complex system in a simple and transparent way, so that river managers may understand and use the model in decision making. In this respect, IBMs and CAs are advantageous because models based on causal rules offer the opportunity to predict outcomes from first principles, whereas models based on statistical correlations to past conditions become progressively less accurate as we move far from the existing data (Willis 2011). Besides, like previously stated, they allow to account for the effect of the state of the modelled species and its environment in the neighbourhood, in

contrast to the theoretical modelling constructs previously used to simulate how animals distribute themselves over suitable habitat, such as the optimal foraging theory, ideal free distribution theory, game theory, artificial neural networks, classification- and regression trees, ultimately to stochastic dynamic programming (Giske et al. 1998, Willis 2011). The fact that in both techniques the environment can be incorporated as a grid of cells poses an excellent opportunity to incorporate environmental data in GIS layers (if necessary in a detailed resolution).

Although IBMs and CAs are both promising methods for spatially explicit and dynamic modelling of fish, they each have their potential advantageous and disadvantageous. The advantageous of IBMs over CA-based models may be the ability to model the population very accurately, because the population is modelled at the level of the individual and it requires fewer assumptions to incorporate information and variation on the interaction of individuals with their environment than a population with its environment. Individuals' paths through complex and dynamic (often chaotic) environments may be simulated, allowing teasing out the balance between passively moving at the mercy of currents (a combination with a hydrodynamic transportation model is then necessary, but also possible), and powered swimming (Willis 2011). However, this requires many parameters and numerical simulations and the empirical knowledge required to parameterize the IBMs tends to be very large (Bauer & Klaassen 2013). One following major hindrance is that IBMs are more or less complex computer simulation models (Grimm et al. 1999). They are hard to develop, hard to communicate, and hard to analyse. Solving this problem requires both software tools which help to implement and communicate IBMs and at least the same effort in analysing the models as is currently put into their development. The complexity also follows from the fact that individual-based ecology is more viewed as an approach for understanding, not simplifying the complexity of nature (Grimm & Railsback 2005). However, when the aim of model development is to use it in decision support, it is important that it is transparent and easy to understand by the end users. Consequently, the biggest challenges in IBM development lies in managing the complexity of the model, without increasing its uncertainty, and communicating the model to the scientific and management community.

The advantage of CA-based models over IBMs is in this respect the ability to model complex systems based on very simple transition rules. The great potency of modelling complex systems follows partly from the ability to combine CAs with other modelling techniques, such as fuzzy logic, artificial neural networks or other data and/or knowledge mining techniques used for instance to quantify the habitat suitability in each cell of the CA grid. The ease of combining these models with CA lies in the discrete nature of space and time. Besides, other modelling techniques may be used to derive the transition rules (Chen et al. 2011). It is a great challenge in developing a CA-based model to find the transition rules that best represent the underlying response of the studied organism to its environment. Since many organisms are not in equilibrium with their environment, it may be difficult to capture the underlying response in which case accurate predictions are not obtained (Rohde 2005). Moreover CA-based models remain difficult to validate. A second disadvantage, following from the discrete nature of space and time, may be the constraints related to the spatial and temporal resolution. A wrong choice of spatial and temporal resolution may have profound negative effects on model results. Chen et al. (2003) have already stated that it is a major challenge and very important to properly couple the different physical and ecological scales of the studied system spatially and temporally.

CHAPTER 3

Study area and data collection

3.1 Introduction

This chapter describes where and how data were collected and how they were analysed to determine pike movement and migration dynamics, habitat use and habitat preference. Since the data on adult pike were collected using radio telemetry, first an overview is given on the main fish telemetry methods applied today to track fish. The field data collected during this thesis could reveal how far adult pike moved per day on average and whether this depended on the time of the year, environmental variables and pike sex, length or weight. Besides, the field data revealed what habitat types were used and preferred by pike and how habitat use and preference varied temporally. The data were used to develop and validate the IBM, to define the habitat suitability in the cells of the CA-based models and to develop a habitat suitability model for adult pike in the river Yser. Section 3.3 describes the parts of the study area and the datasets that were used for the model evaluations in chapters 4, 5 and 8.

The analyses based on the radio telemetry data were described in chapter 6 and 7 and were based on the following research questions:

Movement and migration dynamics:

- Did adult pike movement vary throughout the year?
- Did adult pike migrate and when?
- How was migration affected by environmental factors such as water temperature, day length and flow, and how did this relation differ with pike sex, length, weight and location in the study area?
- What is the expected error in the data related to the adopted sampling protocol?

Habitat use and preference:

- Which macrohabitats were used by adult pike in winter and spring?
- Which mesohabitats were used by adult pike in winter and spring?
- Did adult pike prefer the riparian habitat and what riparian habitats were preferred?

3.2 Fish telemetry

3.2.1 Definition

An understanding of the physiology, behaviour and energetic status of unrestrained organisms in their natural environment is fundamental to basic and applied ecology (Cooke et al. 2004). Over the past half century, wildlife research has relied on technological advances to gain additional insight into the secretive lives of animals. The revolution started in the 1960s with the development of radio telemetry and continues today with the use of GPS-based research techniques (Miller et al. 2010), allowing to monitor and to map details on animal movement and enabling a quantitative analysis of these data even for highly cryptic organisms (Cagnacci et al. 2010).

Although terminology has varied, the set of techniques most appropriate for monitoring remotely can be referred to as biotelemetry (Cooke et al. 2004), or when the remote measurement does not entail the recording of internal physiology or external physical chemical variables simply: telemetry. The direct translation from the Greek ‘*tele*’ and ‘*metry*’ is ‘*remote*’ and ‘*measurement*’, respectively, or in full: “*The remote measurement of data*”. This is also the definition given for telemetry by Cooke et al. (2004) and he added to this that telemetry generally has been assumed to include devices that store data on board (archival data loggers) for later downloading or transmission. Accordingly, Kenward (2000) defined telemetry as the transmission of information about the physiology or behaviour of wild or captive animals, but he defines the locating of the animals as ‘tracking’ instead of ‘telemetry’.

3.2.2 Tag types and techniques

Generally, one performs telemetry to study the behaviour (movement, habitat use and space use) and physiologic and environmental state of animals in places where they cannot easily be observed. Researchers use telemetry tags for this that can either have sensors or not. The tags can store information coming from the sensors or they can immediately transmit this information to a satellite or a receiving device. Many types of data can be stored. Depending on the tag characteristics, different types of telemetry can be defined (Table 3-1). Each type has its specific advantages and drawbacks, which make the technique less or more suitable to apply depending on the study purpose and setting.

The main characteristics distinguishing the techniques are the type of data that can be obtained, the way they are handled and how they are retrieved. All tags are developed to retain data on the animal’s location, but some tags can additionally measure data on the physiology of the studied animal, such as its body temperature or heart rate, or environmental data, such as water temperature or depth (Table 3-1). Data on physiology and environment are measured by specific sensors, that are not present in tags that only record or indicate the animals’ location. The data can either be archived in the tag or immediately transmitted. Some tags archive the data when they are underwater and transmit them to satellites or a receiver when they reach the water surface or are brought into air (Table 3-1). The way the data are recovered highly depends on the tag type and largely determines whether the techniques suits well or not for application in a study. Generally, one can distinguish four main ways of data recovery: passive, when the scientists receives the data in the lab via email from satellites, active by recovering the receivers that archived data, active by recapturing the animal to retrieve the tag that archived data and active by approaching the animal close enough to receive the transmitted signal. Another characteristic that follows from the tag type but may strongly determine the suitability of a telemetry technique is the type of signal that is used to locate the tag or transmit the data. Generally, in satellite telemetry tags transmit data to satellites in the form of electromagnetic pulses via their

antenna. This type of signal can only be transmitted through air, so the antenna has to reach the water surface before any information can be transmitted to the satellite. Consequently, fish or other aquatic animals that never come to the surface cannot be tracked with simple GPS tags. To study these animals, tags were developed that are placed on the outside of the animal and pop off at a pre-programmed time, mainly named pop-off archival tags (PAT) or pop off satellite archival tags (PSAT). The tag floats to the water surface after popping off and transmits the data to a satellite that it has been measuring for weeks without ever transmitting. This telemetry technique has been applied numerous for studying the migratory behaviour and habitat use of sharks (Beguer-Pon et al. 2012, Hammerschlag et al. 2011, Queiroz et al. 2010, Rogers et al. 2013), tuna (Galuardi & Lutcavage 2012) and eels (Aarestrup 2009, Beguer-Pon et al. 2012, Schabetsberger et al. 2013).

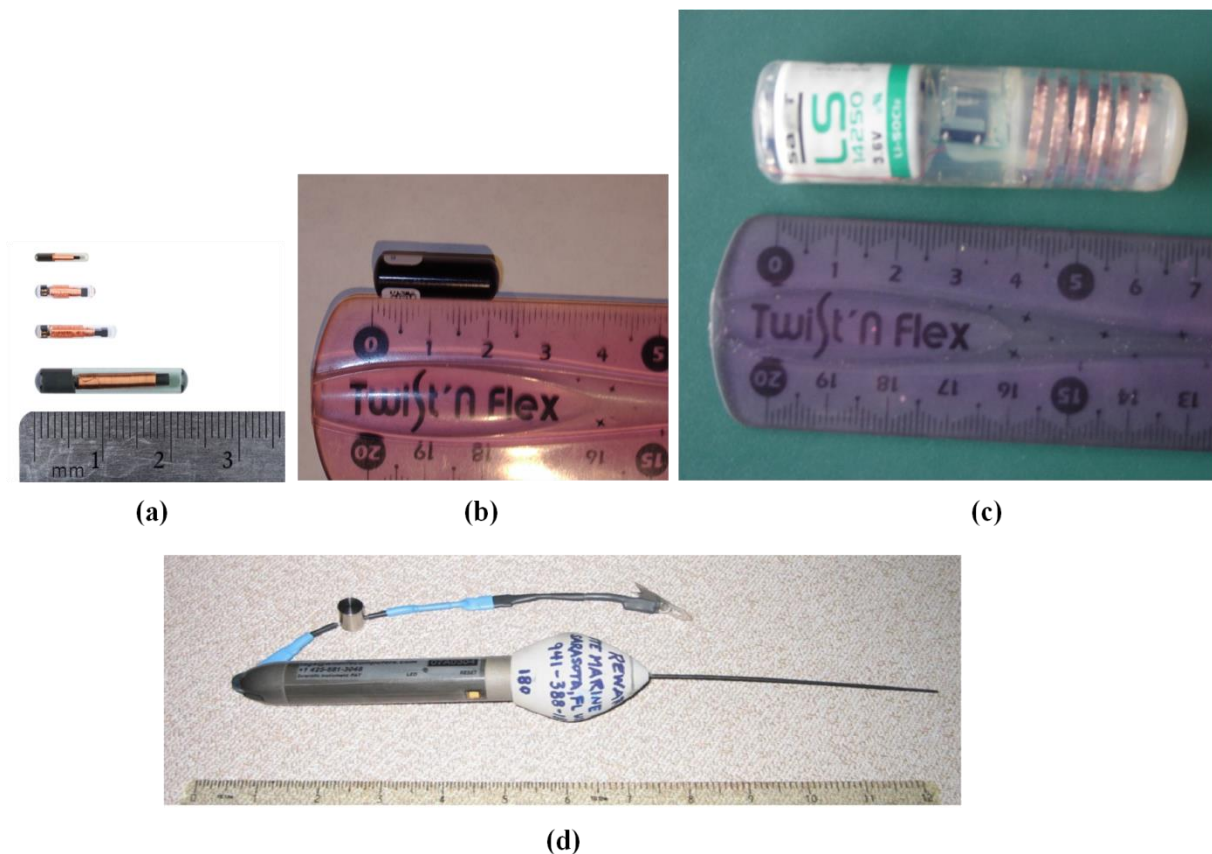


Figure 3-1: Illustration of the size of four tag types: PIT tag (a; source: www.biomark.com), acoustic tag (b; source: Ine Pauwels), VHF tag (c; source: Ine Pauwels) and PAT or PSAT tag (d; source: www.hondouras.com).

The other types of signals that exist beside electromagnetic pulses are acoustic pulses and radio waves. Acoustic pulses, produced by acoustic tags are sounds or ‘pings’ that are picked up by underwater listening devices, called hydrophones (Table 3-1). The hydrophones must be near the animal, or the animal has to pass the hydrophone close enough to pick up the sound. The tags can transmit the acoustic pulse form inside or outside the animals’ body, but most acoustic tags are implanted. Acoustic telemetry works well for animals that permanently live underwater, but the technique does not allow precisely locating the tagged animal, so it suits less for detailed analysis of fish habitat use. Furthermore, since fish have to approach the hydrophones, it neither suits for analysis of far migrating fish in large lakes, seas or oceans. Acoustic tags have already been applied in research on numerous species of fresh water and marine fish (Kilfoyle & Baggeroer 2000, Marshall et al. 2011, Sakabe & Lyle 2010, Walsh et

al. 2012). Radio waves pulses are produced by radio tags, also named very high frequency (VHF) tags. Each transmitter can have a unique frequency, which is received by an antenna that is attached to a receiver (Figure 3-2). The receiver, like a radio, has to be tuned to the specific frequency and makes a beeping sound when it picks up the pulse. The beeping sound gets louder the closer the antenna approaches the radio tag. Triangulation is used to precisely position the fish to 1 to 4 m² depending on the distance between the tagged fish and the observer (Koehn et al. 2012). As in acoustic telemetry, the receiving antenna has to be close enough (depending on the antenna this ranges from a few to 200 m) to the radio tag to pick up the radio wave pulse. The tags can have external or internal transmitting antennas. External antennas have to be placed outside of the fish, while tags with internal antennas are mostly implanted in the fish body cavity. In contrast to acoustic pulses, radio wave pulses can be transmitted to air and water as long as the water has a conductivity that is below or equal to 1000 $\mu\text{S}.\text{cm}^{-1}$. Radio telemetry was applied in this study to enable the detailed localisation of the pike. Lastly, tags exist that produce an identification code that can be read with a scanner, named passive integrated transponder tags (PIT tags). The PIT tag consists of an antenna coil of specially coated copper wire and the scanner contains an excitor coil, through which current is driven that creates an electromagnetic field, energizing the tag within the read range. The tag modulates a signal in the form of an ID code and sends this back to the receiving coil, where the ID code is converted to a digital form, displayed as a numeric or alphanumeric number. The signal transmission can be easily done through soft and hard tissue, such as liquids, glass, plastics and even metals. The PIT tags are generally very small (Figure 3-1), up to minimally 11 mm long (Das Mahapatra et al. 2001). The scanners have to approach the tags (or vice versa) to maximally 0.9 m to read the identification code.

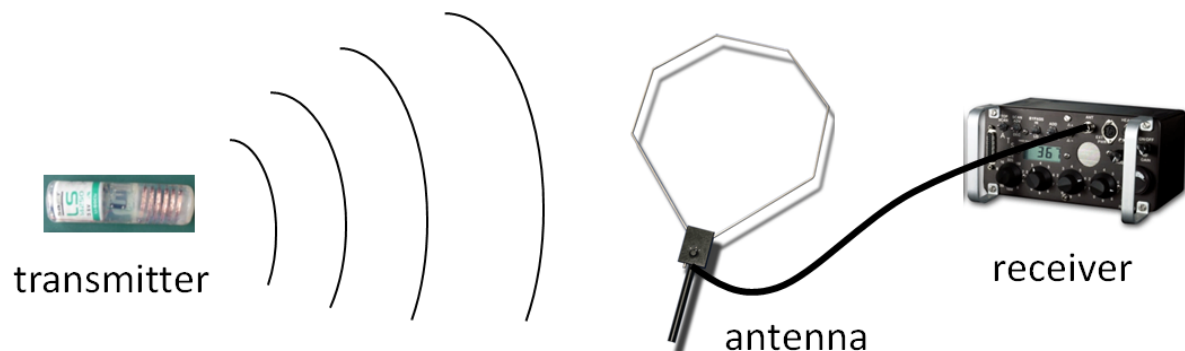


Figure 3-2: The principle of radio telemetry: a tag/transmitter is inserted in or attached to the studied animal and induces signals in the form of radio waves at a unique frequency. The waves are transferred through an antenna to a receiver. The receiver amplifies the electrical signal from the antenna if the receiver is installed at the frequency of the transmitted waves. Tags/transmitters range in size and may have an internal coil antenna or external antenna. The electrical signal from the receiving antenna is transferred to the receiver through a coax cable.

In this research we tracked adult pike using VHF tags (radio telemetry). Beside radio telemetry, only acoustic telemetry suffices to determine the habitat use of the pike to around 4 m² precise. Pike lives permanently below the water surface, so satellite tags would never transmit information on the pike's location. PIT telemetry with permanently installed cables of the receiving devices only allows to localise the pike at the locations of the cables. PIT telemetry with mobile receiving devices requires the mobile cable to be in the water to detect PIT tags and the detection range is too small to detect passing fish in the river Yser, which is 3 to 4 m deep at certain locations. Both are in contrast to the antenna of radio telemetry.

Precise localisation with acoustic telemetry in this study area of > 60 km of accessible river channels, would only have been possible with a dense and extensive network of hydrophones. By the time this study started budget and experience were lacking to properly organise a hydrophone network. In contrast, radio telemetry allowed to analyse the habitat use of the pike to maximally 4 m² precise with relatively few devices.

Table 3-1: Overview of tag types and their characteristics regarding the handling of the data (storage or transmission), the data type (data on the location or the physiology of the animal or environmental data) and data recovery (recovery or approach of the tagged animal, recovering the tags only or passive reception of the data without animal or tag approach or recovery) beside information on the medium that is needed to transmit the signal (water and/or air), the signal type and the size of the tags (adapted from www.sealtag.org).

Tag name	Data handling	Data type	Data recovery	Signal	Data transmission medium	Tag size *
Archival tags	Archiving	Location, physiology, environment	Tag recovery by animal recovery	-	-	
Archival-satellite tags	Archiving and Transmission	Location, environment	Passive data recovery by satellite	Electromagnetic pulses	Air	Sizes from 80 x 50 x 25 mm onwards
PAT or PSAT tags ¹	Archiving and Transmission	Location, environment	Tag recovery by tag pop up and satellites	Electromagnetic pulses	Air	Smallest: 115 mm long
LHX tags ²	Archiving and Transmission	Location, environment	Passive data recovery by satellite	Electromagnetic pulses	Air	
Satellite tags	Transmission	Location, environment	Passive data recovery by satellite	Electromagnetic pulses	Air	
GPS tags	Transmission	Location	Passive data recovery by satellite		Air	Smallest: 50 x 40 x 10 mm
VHF tags ³	Transmission	Location	Active data recovery by approaching the animal	Radio wave	Air and fresh water (conductivity < 1000 $\mu\text{S}\cdot\text{cm}^{-1}$)	Large range of sizes, depending on the battery size
VHF archival tags	Archiving and transmission	Location, temperature, depth and activity	Active data recovery by approaching the animal	Radio wave and electromagnetic pulse	Air and fresh water (conductivity < 1000 $\mu\text{S}\cdot\text{cm}^{-1}$)	Smallest available: 24 x 19 mm
Acoustic tags	Transmission	Location and environment	Passive or active data recovery by hydrophones over small distances	Acoustic pulse	Water	Generally smaller than VHF tags, up to only 20 x 5 x 2 mm in size
PIT tags ⁴	Transmission	Location	Active data recovery by tag reader over very	Electronic identification	Air	Up to 11 mm

small distance	code
*: Sources on tag size: www.wildlifecomputers.com , www.atstrack.com	
1: Pop-up Archival Tags (PAT) or Pop-up Satellite Archival Tags (PSAT)	
2: Life History Transmitters (LHX)	
3: Very High Frequency (VHF)	
4: Passive Integrated Transponders (PIT)	

3.3 Study area

Pike were studied in the 1101 km² drain area of the 44 km long Belgian part of the river Yser (Figure 3-3). The river has a rainfall-dominated hydrology with an average annual flow of 1.44 m³ s⁻¹, a peak flow of 5.7 m³ s⁻¹ and a base flow of 0.8 m³ s⁻¹ (Mouton et al. 2012a). The river is navigable and a tidal sluice at the estuary prevents tidal water level fluctuation and inflow of salt water. Directly upstream of the tidal sluice the river flows in a 370 x 1000 m wide basin with a depth of 7 m. There is no migration barrier in the main river, and pike can freely move between the main river and most of its tributaries. Average water depth is 2.5 m (Mouton et al. 2012a) with the river thalweg varying in depth from 2.8 to 5 m. Near the French border, the river is 8 to 10 m wide, at the mouth it is 25 m wide (Mouton et al. 2012a). In the river Yser, 58% of the river banks were originally artificially embanked, because a significant area of the floodplain lies below sea level. Due to this canalisation, depth, substrate and flow velocity are distributed relatively uniformly. To restore the riparian habitat and the associated fish populations, the river managers constructed several artificial foreshores and river side arms between 2002 and 2005.

The water quality of the river Yser varies little throughout the year (Flemish Environment Agency, www.vmm.be). The conductivity averages 0.75 mScm⁻¹ but can exceed 1 mScm⁻¹ in extremely dry periods. The fish fauna in the study area consists of 24 species, however not all 24 species are present everywhere in the study area. The most dominant species, occurring everywhere in the study area and being dominant in numbers and biomass are white bream (*Blicca bjoerkna* L.), roach (*Rutilus rutilus* L.), European eel (*Anguilla Anguilla* L.), freshwater bream (*Abramis brama* L.) and common carp (*Cyprinus carpio* L.). Two dominant predators beside pike are European perch (*Perca fluviatilis* L.) and pikeperch (*Sander lucioperca* L.; see INBO, www.vis.inbo.be, for the full species list). Fisheries legislation prohibits fishing from March 1st to May 31st in the tributaries of the river Yser, however, on the main river fish can be caught throughout the year. All fish have to be released immediately after they were caught.

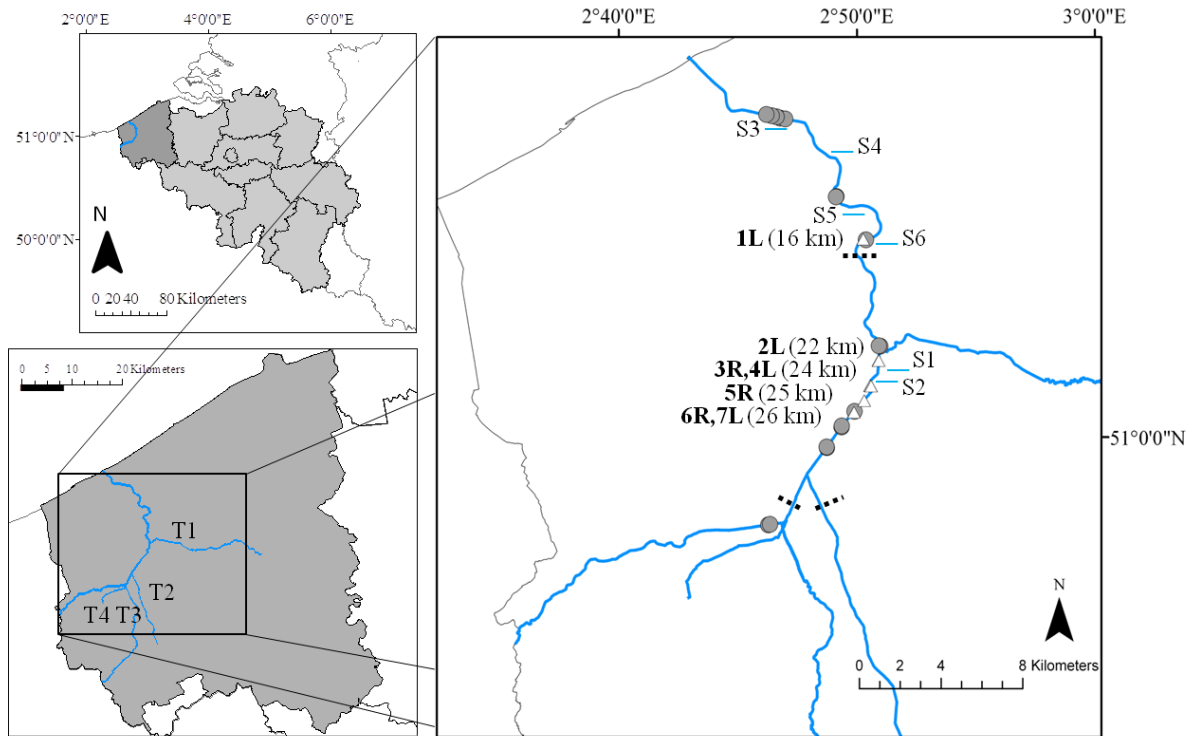


Figure 3-3: The Belgian part of the River Yser (navigable river), in Flanders (Belgium) and the fyke locations. Capture locations are described by an index (1 to 7), the position of the fyke near the left (L) or right (R) bank and the distance to the tidal sluice at the river mouth (km). Locations where temperature was logged are marked by a dotted line (T1 = Handzamevaart (around 10 m wide), T2 = Canal from the city of Ieper to the River Yser (navigable river), T3 = localisation of the Landdijkgracht (around 5 m wide), which is a tributary of the larger Kemmelbeek (around 7 m wide), T4 = Boezingegracht (around 5 m wide); white triangles = pike caught for tagging, grey dots = no pike caught by fykes, horizontal lines = locations of river side arms: S1-S2 = natural river side arms and S3-S6 = artificial river side arms).

In this thesis we investigated pike habitat use and preference at the meso and macro-scale. At the meso-scale, eight different riparian habitat types were defined based on a combination of the vegetation types and river bank types (Table 3-2). The riparian vegetation in the study area can be classified as bare (B), reedy (R) and woody (W) vegetation. Three river bank types, characterised by a different degree of anthropogenic disruption, are present in the study area: artificial vertical banks (AVs; high disruption), artificial foreshores (AFs; moderate disruption) and semi-natural banks (SNBs; low disruption). AVs are vertically straightened and reinforced with concrete, while AFs consist of a row of 0.2 m diameter wooden posts that are positioned in the river channel between 0.7 m and 2.5 m from the river bank. The posts are placed at 0.05 to 0.2 m distance from each other to protect the riparian habitats from shipping wave action. Vegetation in the zone between the posts and the river bank consists mainly of reed and vegetation cover ranges from 0 to 100%. SNBs are highly heterogeneous and characterised by varied bank vegetation such as trees, reed and other emergent vegetation (Mouton et al. 2012a). The combination of the different vegetation and river bank types led to eight different riparian habitat types in the study area: bare, reedy and woody artificial vertical banks (B:AVs, R:AVs and W:AVs, respectively), bare, reedy and woody semi-natural banks (B:SNBs, R:SNBs and W:SNBs, respectively) and bare and reedy artificial foreshores (B:AFs and R:AFs, respectively; Figure 3-4).



Figure 3-4: Riparian habitat types present in the river Yser and its small and large tributaries (Figure 3-3): bare artificial vertical bank (B:AV; (a)), reedy artificial vertical bank (R:AV; (b)), woody artificial vertical bank (W:AV; (c)), bare semi-natural bank (B:SNB; (d)), reedy semi-natural bank (R:SNB; (e)), woody semi-natural bank (W:SNB; (f)), bare artificial foreshore (B:AF, (g)), reedy artificial foreshore (R:AF, (h)); sources: <https://www.google.be/maps> (a to f), De Rycke et al. 2006 (g) and Ine Pauwels (h)).

At the macro-scale, five different habitat types were distinguished: the main river, the large and small tributaries and the artificial and natural side arms. The main difference between the large and small tributaries is their width and depth. The two largest tributaries of the river Yser (the Handzamevaart (T1) and the Ieper-Yser Canal (T2); Figure 3-3) are 10 to 15 m wide and 1 to 2.5 m deep, whereas the small tributaries are 4 to 10 m wide and maximally 2 m deep. Two small tributaries that were used by tagged pike are the Landdijkgracht (T3) and the Boezingegracht (T4); Figure 3-3). Side arms are shallow (0.5 to 1.5 m deep) and stagnant, with banks that are dominated by tall herbs and reed, and are connected to the main river. Two of the six side arms in the study area are natural (S1 to S2; Figure 3-3) and two are artificial (S3 and S6; Figure 3-3). The artificial side arms were created between 2002 and

2005 to restore the riparian habitat in the river Yser. Although they are relatively young, the reed vegetation is similar to the reed vegetation in the natural side arms. All side arms in the study area are between 150 and 500 m long and between 10 and 20 m wide. All meso-scale riparian habitat types are present in the main river. The two largest tributaries are characterised by B:SNBs, R:SNBs and W:SNBs, except the most downstream part of T1 in the city of Diksmuide that consists of B:AVs and R:AVs. The riparian habitat types in the small tributaries are B:SNBs, R:SNBs and (less abundant) B:AVs.

Water temperature was logged every 30 min at three locations in the study area by Tidbit temperature loggers (Onset) with an accuracy of 0.01° C. The average, minimum and maximum temperature measured and averaged over these three locations between November 2010 and December 2011 were 12.5, -0.14 and 24.70 °C, respectively (Figure 3-6). Daily flow data ($\pm 0.01 \text{ m}^3 \text{ s}^{-1}$) were provided by the Hydrographic Information Centre (HIC, www.waterinfo.be). Flow and flow velocity (m.s^{-1}) data are available for two locations in the river Yser, of which one is outside the area used by the tagged pike. Therefore, only flow data of the most downstream location were used in this study (Figure 3-3). The average, minimum and maximum flow (and flow velocity) measured between November 2010 and December 2011 were 6.96 (0.09), 3.21 (0.04) and 50.71 $\text{m}^3 \text{ s}^{-1}$ (0.56 ms^{-1}), respectively (Figure 3-6).

Water temperature regimes were used to divide the study period into winter (water temperature below 5°C, November 26th to February 4th) and spring (water temperature between 5 and 15°C, February 5th to April 19th). This division was based on the findings that pike start spawning migration around 5-6 °C (Ovidio & Philippart 2003), spawn at water temperatures between 6 and 14 °C (Raat 1988b) and tend to decrease their activity around 0 °C (Vehanen et al. 2006). Water temperature was logged every 30 min at three locations in the study area by Tidbit temperature loggers (Onset) with an accuracy of 0.01 °C (Figure 3-3).



Figure 3-5: Macro habitat types present in the study area (Figure 3-3): the main river (a; source: <http://blog.seniorennet.be>), large tributaries (b; Canal Ieper-Ijzer, source: <http://nl.wikipedia.org/wiki/Ieperlee>), small tributaries (c; Boezingegracht, source: <http://siagrius.be/siagrius>), artificial side arms (d; Mannekensvere, source: <http://www.inbo.be>) and natural side arms (e; Oud-Haantje Diksmuide, source: <http://www.google.be/maps>).

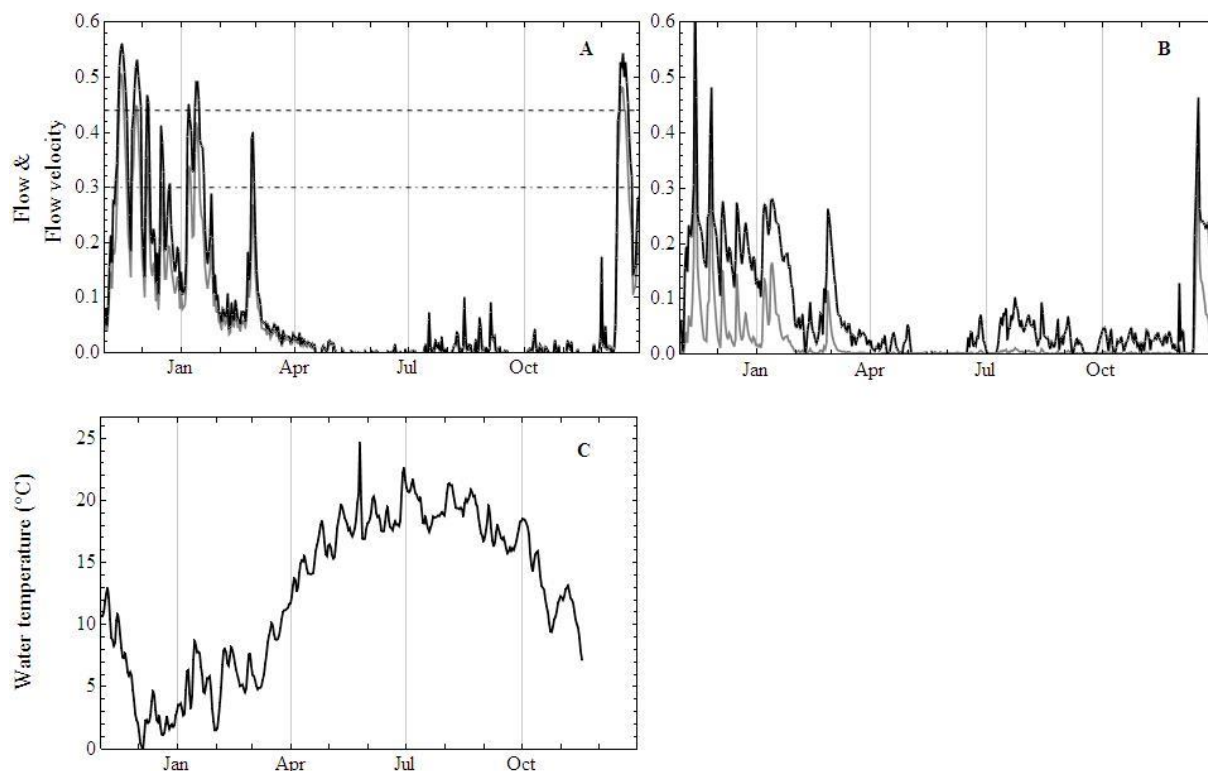


Figure 3-6: Flow ($\text{m}^3 \text{s}^{-1}$; black line in A and B), flow velocity (ms^{-1} ; grey line in A and B) and water temperature ($^{\circ}\text{C}$; C) from October 2010 till December 2011 in the downstream part of the river Yser (Keiem; A), the upstream part (Roesbrugge; B) and averaged over three locations in the river Yser and the Canal from Ieper to the river Yser (C; see Figure 3-3 for the locations).

The CA and IBM model evaluations described in chapters 4 and 5 were based on data of a 10 km stretch of the 44 km Belgian part of the river Yser (Figure 3-7). In this 10 km river part, one artificial and two natural spawning grounds are located at 158, 8225 and 8896 m upstream of the downstream boundary of the river stretch, respectively. The hydraulic and physicochemical properties only negligibly varied in this 10 km river stretch (Figure 3-8). These data were obtained from the Flemish Environment Agency (VMM; www.vmm.be)

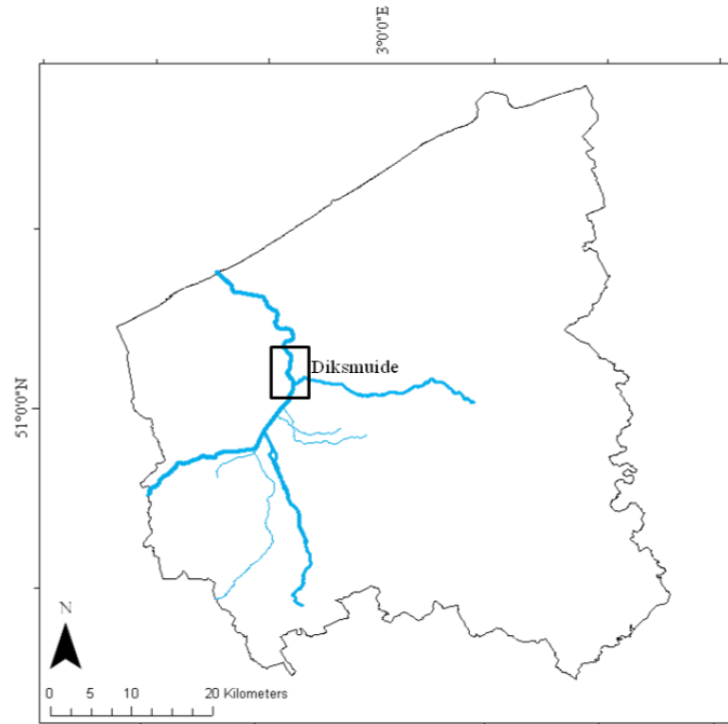


Figure 3-7: Location of the 10km study area (box) in the Belgian part of the river Yser.

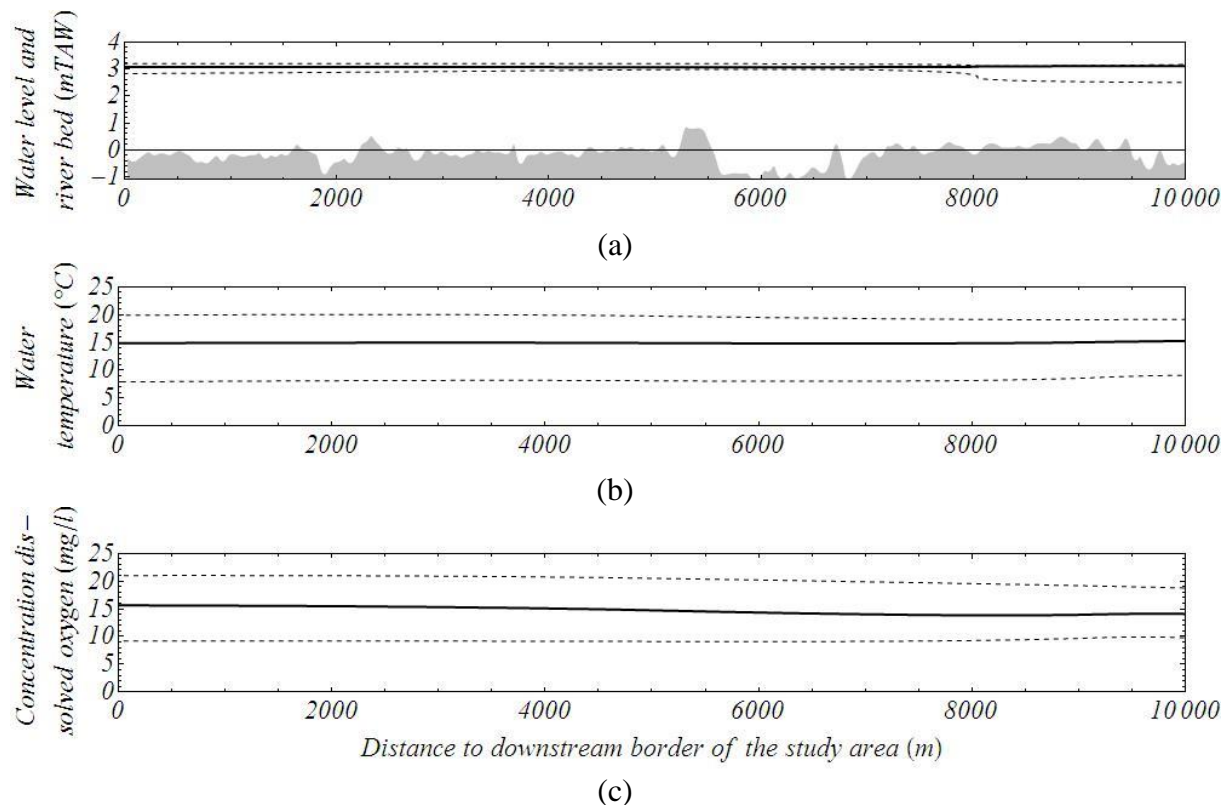


Figure 3-8: Average water level (a), water temperature (b) and dissolved oxygen concentration (c) versus the distance from the downstream border of the study area during March 21 – June 21 2009 and 2010. The dashed lines enclose all measurements.

For the development of the habitat suitability model (HSM), described in chapter 8, data on the study area till 1 km upstream and downstream of the most upstream and downstream pike observations, respectively, in the main river and the tributaries were used (Figure 3-9).

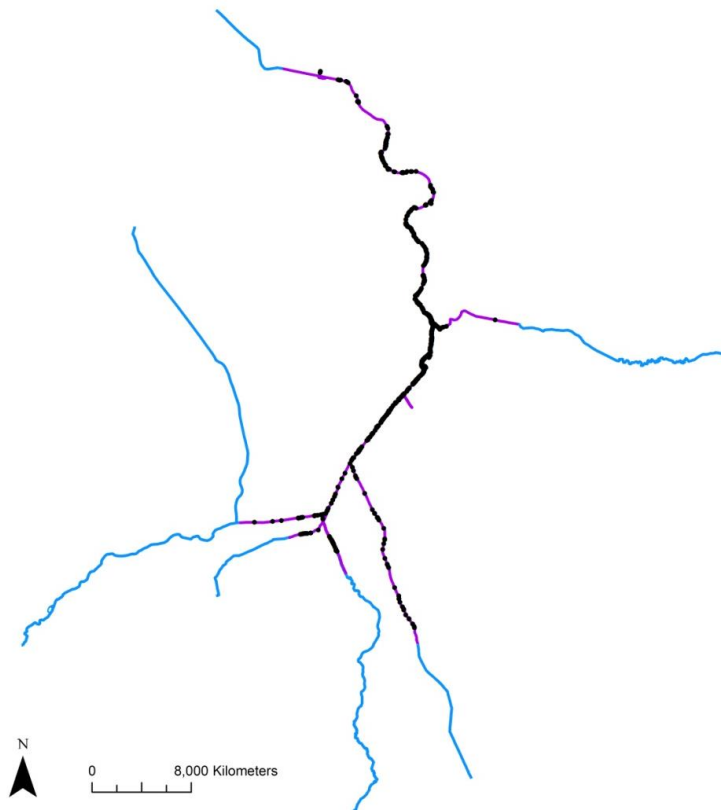


Figure 3-9: Indication of the area studied in the HSM (purple line: part of the study area used for the HSM development; blue line: the river Yser from Dutch-French border till the estuary and the five largest tributaries (see chapter 3); black dots: pike observations).

Table 3-2: Overview of the study area, data used and aim of the analyses in chapters 4 to 8.

Chapter	Study area	Dataset	Collection	Aim	Main question
4	10 km river stretch (Figure 3-7)	Vegetation type River bank type	Visually assessed Visually assessed	Evaluation of the applicability of the CA modelling paradigm	Is the model sensitive to the grid resolution, the total number of pike and their initial distribution?
5	10 km river stretch (Figure 3-7)	Vegetation type River bank type	Visually assessed Visually assessed	Evaluation of the applicability of the IBM modelling paradigm	How well can pike migration be simulated based on individual characteristics?
6	Belgian part of the river Yser (Figure 3-3)	Adult pike Juvenile pike Water temperature Flow	Radio telemetry Fyke and electro INBO HIC	Analysis of the movement and migration dynamics of adult pike	What environmental variables affect pike migration and how?
7	Belgian part of the river Yser (Figure 3-3)	Adult pike Juvenile pike Vegetation type River bank type Macrohabitat type	Radio telemetry Fyke and electro GIS map INBO GIS map INBO Visually assessed	Analysis of the habitat use and habitat preference of adult pike at the macro – and mesoscale	What macrohabitats and what riparian habitat types does pike use and what riparian habitat types are preferred?
8	Belgian part of the river Yser, tributaries and side arms till 1 km up- and downstream of the most up- and downstream pike observation, respectively (Figure 3-9)	Adult pike Vegetation type River bank type Macrohabitat type Depth	Radio telemetry GIS map INBO GIS map INBO Visually assessed Visually assessed	Development of a rule base indicating the habitat suitability for adult pike of the river habitat	What habitat variables, out of riparian vegetation type, bank type, macrohabitat type and depth define adult pike habitat suitability most and is there a seasonal difference?

3.4 Data collection

3.4.1 Adult pike capture and tagging

Although historical evidence of a high-density population of pike in the river Yser exists (De Nayer & Belpaire 1997), densities have been low since the first standardised observations in 1996 (INBO, www.vis.inbo.be). For the tracking study, pike were sampled at 15 different locations in the river between 3 and 32 km upstream of the tidal sluice (Figure 3-3) by fyke sampling during nine events between November 24th and December 13th 2010. At each sampling location, two double fykes were placed in the river for 48h. In total, nine females and six males were caught at five different locations during seven different sampling events (Table 3-3). Data of twelve of these pike were used for analysis (see section 3.5 and Table 3-3). The pike were anaesthetised immediately in a 1:9:10000 clove oil:ethanol:water solution (C8392, Sigma, Bornem, Belgium), measured, weighed and tagged with a 68 mm long and 18 mm wide body implant radio transmitter (Model: F1230, coil antenna, Advanced Telemetry Systems Inc., Isanti, MN, USA; weight: 23 g in air, battery life: 502 days). Each transmitter had a different frequency between 40000 and 41000 MHz. The fish ID used per pike further in this research indicates the transmitted frequency. The average female and male mass and length were 4213 ± 2889 and 4832 ± 2640 g, and 75 ± 16 and 81 ± 12 cm, respectively. Thus, the transmitters never exceeded 2% of the body mass (Jepsen et al. 2002). The transmitters were inserted into the body cavity through a ventral 20-25 mm incision between the pelvic girdle and the anal fin, which was then closed with three sutures. The sex was determined during surgery by gonad inspection. The duration of the operations ranged from 5 to 10 minutes, and the pike needed about 10 minutes to recover. One hour after recovery the pike were released at their catch location.

Table 3-3: Overview of the biometric data of fifteen pike in the Belgian part of the River Yser. Bold: pike investigated in a 24h sampling campaign in winter (^w), spring (^s) and/or summer (^{su}). 24h data are not included in the number of observations, mean MDD and total movement. Data of pike that were lost before the spawning period (*) or were relocated less than 25 times () were omitted from statistical analyses.**

Sex	Time of tagging	Length at tagging (cm)	Weight at tagging (g)	Number of observations (in winter and spring)	Fish ID (Freq. in MHz)	Catch location (Figure 3-3)	Mean MDD (STDEV) (m day ⁻¹)	Total observed movement (m)
F	13/12/2010	60	1057	79 (62)	40.600^{w-su}	3	658 (1230)	87170
M	1/12/2010	97	8150	91 (66)	40.611^w	3	114 (171)	25155
F	26/11/2010	55	1124	71 (63)	40.620	3	155 (210)	22600
M	10/12/2010	68	2350	69 (67)	40.630	2	640 (1051)	74116
F	2/12/2010	99	8750	74 (72)	40.651^w	2	1171 (1447)	107094
M	2/12/2010	67	1100	84 (62)	40.671^{w-s-su}	5	212 (384)	43159
F	24/11/2010	70	2927	61 (59)	40.681^w	3	273 (324)	28781
F	2/12/2010	85	5600	75 (69)	40.781^w	2	428 (734)	64502
M	10/12/2010	82	5010	77 (58)	40.801	2	605 (957)	109764
F	6/12/2010	59	1700	82 (55)	40.811^{su}	4	434 (639)	66588
M	1/12/2010	83	6070	83 (63)	40.820^s	3	569 (1034)	110585
F	24/11/2010	78	3700	60 (59)	40.841	1	786 (1001)	85256
F	1/12/2010	78	4430	29 (29)	40.661 *	5	1734 (2044)	79262
M	1/12/2010	89	6310	30 (30)	40.771 *	3	1187 (2202)	73526
F	10/12/2010	96	7340	17 (17)	40.831 **	2	491 (440)	43119

3.4.2 Pike tracking

Regular tracking

Pike observations were obtained by radio tracking manually from land with a magnetic dipole antenna (Advanced Telemetry Systems Inc., Isanti, MN, USA) to firstly track the pike at a precision of 2000 m². Subsequently, a low frequency loop antenna (Advanced Telemetry Systems Inc., Isanti, MN, USA) was used to localise the pike by triangulation (Diana et al. 1977; Jepsen et al. 2001) at a precision of 1 to 4 m² depending on the distance between the pike and the observer. The antennas were connected to a R2000 receiver (Advanced Telemetry Systems Inc., Isanti, MN, USA) that searched each frequency at 4 s intervals. The exact pike position was recorded on a 1:500 map of the study area.

Pike were tracked between November 2010 and December 2011. Tracking frequency differed between seasons due to practical problems from the end of spring till midsummer. During winter and spring routine monitoring consisted of tracking the pike every two days. During two periods this tracking frequency was increased to daily trackings: immediately after each pike was tagged until January 1st, to avoid loss of pike due to potentially higher activity after tagging, and in February and March, which is generally recognised as the spawning period (Craig 1996) when higher pike activity may occur. At the end of spring tracking of 4 individuals in the downstream part of the main river was restrained by water conductivities above 1.0 mS. Consequently, the tracking frequency of the other 8 pike was lowered to one to two trackings per week in summer and autumn.

During each tracking campaign pike were tracked along 47 km of main river, tributaries and side arms. When pike were missing, they were searched in the small tributaries.

24 h tracking

During three 24 h tracking campaigns in winter, spring and summer, respectively six, two and three adult pike (Table 3-5) were observed every 30 min by manual trackings from land with a low frequency loop antenna (Advanced Telemetry Systems Inc., Isanti, MN, USA). The data were used to evaluate the movement of the pike between two daily observations by determination of the time to independence (TTI; Box 3-1).

Box 3-1: Time To Independence

Definition

To have a representative dataset on the animal's behaviour it is necessary in every telemetry study to (A) test the autocorrelation between successive observations and (B) question what the time interval is at which autocorrelation of observations is negligible. This time interval is named the time to independence (TTI; Hodder et al. 2007) and it is the time interval for which the first observation cannot predict where the second will be. On the one hand information on the TTI helps to optimise the tracking protocol, balancing the need for sufficient observations per individual with a feasible sample of animals. On the other hand it is necessary to estimate the potential loss of information following gaps in the dataset due to problems with observing an animal at a specific time.

Method

A method to test for independence (A) and determine the TTI (B) was developed by Swihart & Slade (1985). The method is based on Shoener's index, which is:

$$V = t^2 / r^2 \quad 3-1$$

where t^2 is the mean squared distance between consecutive location records and r^2 is the mean squared distance from each location to the range centre. The range centre is the arithmetic mean of all coordinates. Shoener (1981) defined t^2 as follows:

$$t^2 = \frac{1}{m} \sum_{i=1}^m (x_{i+1} - x_i)^2 + \frac{1}{m} \sum_{i=1}^m (y_{i+1} - y_i)^2, \quad 3-2$$

where m is the number of pairs of successive observations ($m = n - 1$ if all pairs are used, where n is the number of observations) and i denotes the order in which observations were collected. Further, Shoener (1981) defined r^2 as follows:

$$r^2 = \frac{1}{n-1} \sum_{i=1}^n (x_i - \bar{x})^2 + \frac{1}{n-1} \sum_{i=1}^n (y_i - \bar{y})^2, \quad 3-3$$

where $\bar{x} = x_i/n$ and $\bar{y} = y_i/n$. Thus, the Shoener's index evaluates the way that the distance between location records changes with sampling intervals (Swihart & Slade 1985). The index is based on von Neumann's ratio, which is a statistic to measure adherence to a Markov process (Swihart & Slade 1985). Von Neumann (1941) considered n successive observations from a normal distribution population with mean μ_x and variance σ_x^2 and he examined the ratio $V = d^2/S^2$ using the slightly biased estimator of σ_x^2 :

$$S^2 = \frac{1}{n} \sum_{i=1}^n (X_i - \bar{X})^2, \quad 3-4$$

and the mean squared difference between successive observations:

$$d^2 = \frac{1}{n-1} \sum_{i=1}^{n-1} (X_{i+1} - X_i)^2. \quad 3-5$$

Important and appealing to this ratio is that based on the normality assumption, V and S^2 are stochastically independent random variables, so that $E(V) = E(d^2)/E(S^2) = 2n/(n-1)$

under the assumption of independence, where E is expected value (Von Neumann 1941). Consequently, for large n (or all n if the unbiased estimator for σ_x^2 is used) observed values of V that are significantly less than 2 indicate positive autocorrelation or aggregation, whereas values larger than 2 indicate independence between observations (Swihart & Slade 1985).

(A) Testing for independence

If the number of pairs of observations is larger than 19 and the time interval between consecutive observations is equal, the following equations can be applied to test for independence of the data (Swihart & Slade 1985):

$$\ln S = -0.0502 + 0.164(e) - 0.0156(e^2) - 0.437(\ln m), \quad 3-6$$

where S is the estimated standard deviation, m is the number of pairs of observations, which is $n - 1$ if all observations are used and e is the eccentricity, which is the ratio of the lengths of the major and minor axes of the home range.

To test the null hypothesis that the observations are independent (i.e. Schoener's index ≥ 2) is true, a one-tailed test is applied at the 75% confidence level ($\alpha = 0.250$) as follows:

$$\text{the critical value} = 2 - (0.675 \times S), \quad 3-7$$

where 2 is the mean of $\frac{t^2}{r^2}$ and 0.675 represents the 75th percentile of the standard deviation (S). If the critical value is greater than the result of equations 3-2 and 3-3 the observations are dependent.

(B) Determining the TTI

If the observations are dependent, the question is what the minimal time interval is between observations to yield independence of the observations (TTI). To answer this question, Schoener's index needs to be calculated for all data that are separated by a specific time interval (k), where k may range from for instance 30 minutes to 24 hours (Swihart & Slade 1985).

The TTI is defined as the smallest k exhibiting a no significant ($\alpha = 0.050$, one-tailed test) Schoener's index and followed by at least two k values with no significant Schoener's indices.

The ratio of von Neumann belongs to an univariate family of distributions, whereas the Schoener's index is a bivariate extension from it. This makes the Schoener's index, in contrast to the von Neumann's ratio particularly useful for application on animal movements that entail movements in the X and Y direction.

The path between consecutive observations in a meandering river is not necessarily straight due to the dimensions of the study area. In this study this was particularly true for the observations of the regular tracking, but not for the observations of the 24 h tracking. Therefore, we applied the Schoener's index on the X and Y coordinates of the 24 h pike tracking but not on the observations of the regular pike tracking.

Result and discussion

Observations that were taken every 30 minutes were dependent at the 95% level for all pike (Table 3-4). The TTI differed between individuals and ranged from 1.0 to 4.0 hours in winter, 1.5 to 2.5 hours in spring and 1.5 to 2.0 hours in summer (Table 3-4 and Figure 3-10).

Table 3-4 TTI for seven pike that were tracked for 24 hours in winter and/or spring and/or summer, and statistical test for dependence of observations with a time interval of 30 minutes. All tests for dependence were significant, which means that the null hypothesis of independence is rejected.

Fish ID (Freq in MHz)	TTI (hours)		
	Critical value $>/<$ Schoener's index		
	Winter	Spring	Summer
40.600	1.0 2.859 > 0.786	-	2.0 2.700 > 0.171
40.611	4.0 4.712 > 0.058	-	-
40.651	2.0 2.573 > 0.379	-	-
40.671	2.5 2.726 > 0.093	1.5 4.735 > 0.432	1.5 2.452 > 0.409
40.681	2.5 4.600 > 0.154	-	-
40.781	2.5 4.776 > 0.072	-	-
40.811	-	-	1.5 2.934 > 0.244
40.820	-	2.5 4.760 > 0.315	-

In all three seasons the Shoener's index increased steadily up to 5 to 10 hours and peaks around 10 to 15 hours. Interestingly, the values declined again from 15 hours onwards, to yield dependent observations again around time intervals of 20 to 24 hours. This may indicate a dial cycle in the movement of the pike individuals. Indeed, six pike were observed at a similar distance from the river mouth after 20 to 24 hours (Figure 3-11).

Although only one individual was tracked in all three seasons, these preliminary results may suggest no difference in TTI between seasons.

Conclusions

The results of these tests indicate that it is not necessary to track adult individual pike every 30 minutes, because this yields dependent observations. To not miss any information on the used locations by the fish, it is desirable to track them every hour. This is indicated by the TTI's of 1 to 4 hours. However, a TTI of 1 hour was only observed for one animal and most animals had TTIs of 2.5 hours. Consequently, if individual pike would have been tracked every 2.5 hours during one dial cycle not much spatial information would have been missed. The test of dependence of the data throughout one dial cycle revealed dependence of the data for all animals after about 20 to 24 hours. Together with the analysis on the location of the animals in the study area, this strongly suggests a cycle in the dial movement pattern of the adult pike. Although more individuals should have been tracked to correctly conclude on this, the results suggest no substantial differences in the TTI and dial movement patterns of the fish between seasons.

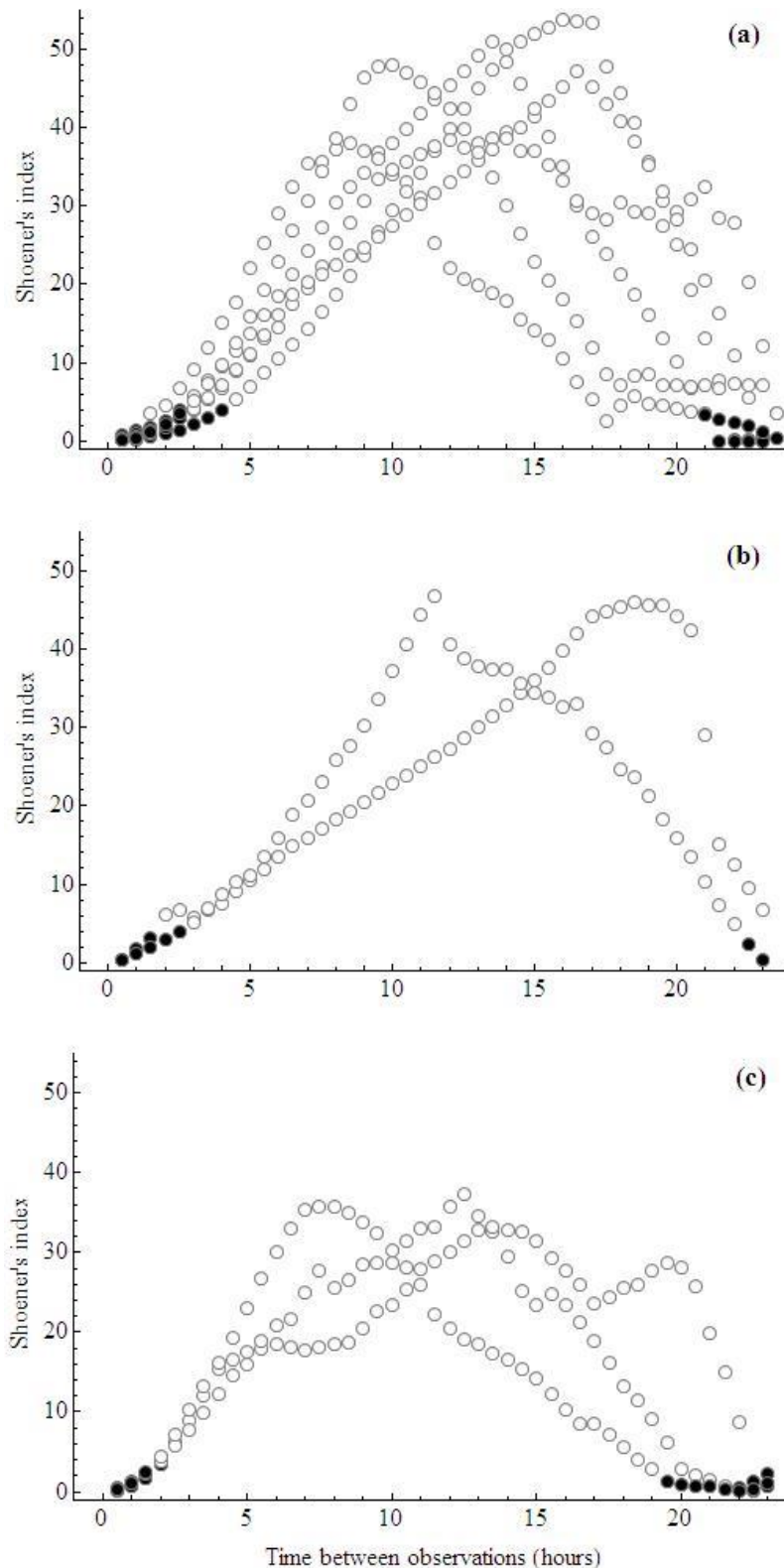


Figure 3-10: Shoener's index as a function of the time interval between observations from 24 h tracking of 6, 2 and 3 adult pike in winter (a), spring (b) and summer (c), respectively. Shoener's index is defined by equations 3-2 and 3-3 and significance was tested using equations 3-6 and 3-7 (Swihart & Slade 1985; black dots: significance and thus dependence of the observations, white dots: no significance and thus independence of the observations).

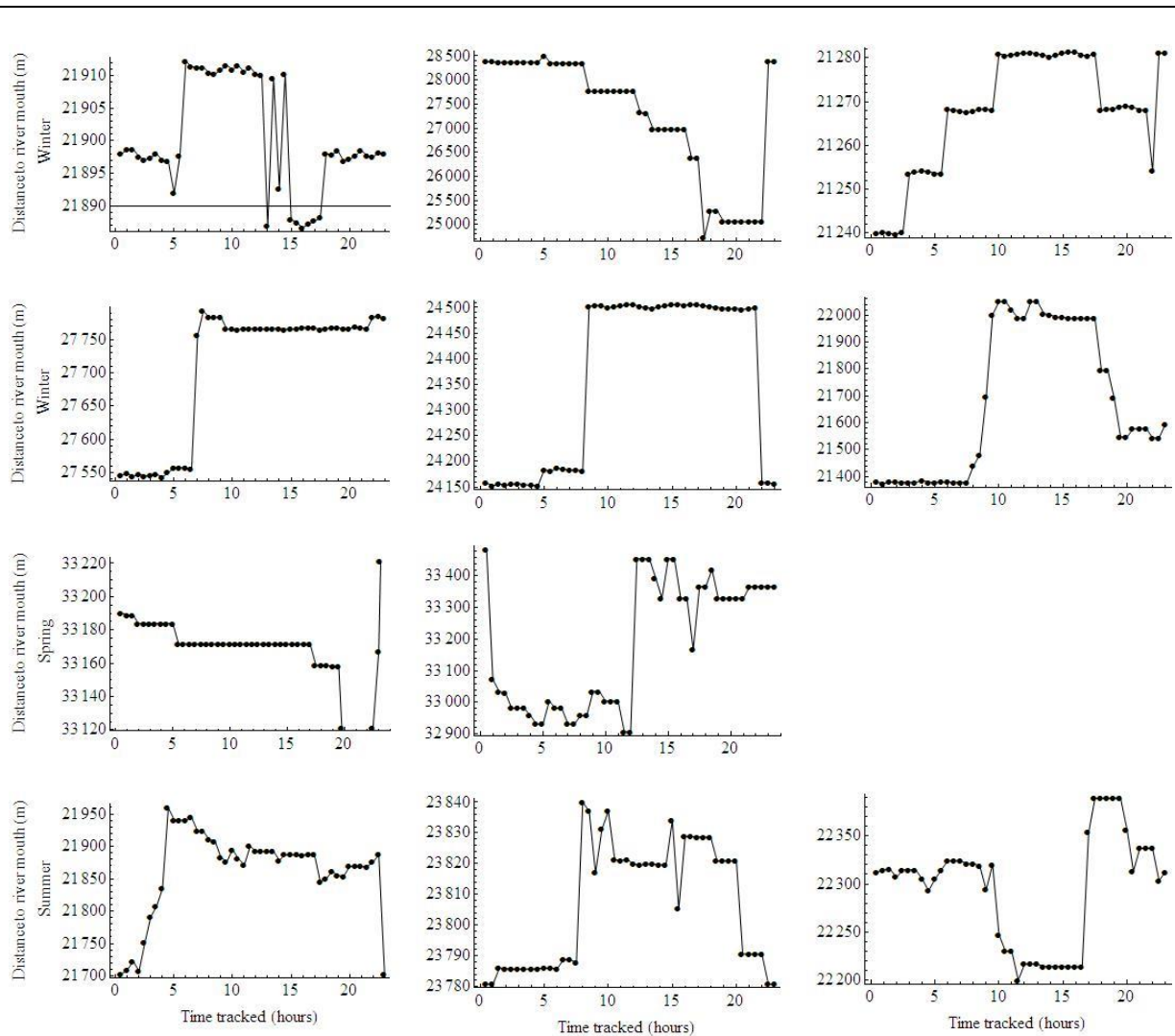


Figure 3-11: Distance to the river mouth of the observations (black dots) of six, two and three adult pike in winter, spring and summer, respectively.

Table 3-5: Total observed movement per 24 h in winter, spring and summer of six, two and three adult pike, respectively.

Fish ID (Freq. in MHz) - Total observed movement (m)		
Winter (January 26 th – 27 th 2011)	Spring (April 12 th - 13 th 2011)	Summer (August 22 nd – 23 rd 2011)
40.600 – 1179	-	40.600 - 1130
40.611 – 3807	-	-
40.651 – 1515	-	-
40.671 – 818	40.671 - 1177	40.671 - 3841
40.681 – 1412	-	-
40.781 - 2389	-	-
-	-	40.811 - 1272
-	40.820 - 3856	-

3.4.3 Sampling of juvenile pike

The presence of YOY was evaluated by an electro and fyke fishing campaign in the river side arms and the tributaries in the study area in May and June 2011. Electrofishing and fyke net sampling efforts in previous research showed that juvenile pike density was very low in the main river (Mouton et al. 2012a). Therefore, we focused on the side arms and tributaries. In total 26 locations were fished, of which five were located in river side arms, 13 in tributaries and eight in tributaries of tributaries (Figure 3-12). Three locations had been visited by tagged adult pike and eight locations were within 500 m of a pike observation. Each of the locations visualised in Figure 3-12 was subjected to sampling by using one-pass electrofishing with a generator and a control box (DECA 3000) that converted a 230V alternating current into a 200V direct current, while a 0.1 m diameter anode was applied to sample the fish. Previous research has shown that juvenile fish are caught more efficiently with this small anode (Baras & Nindaba 1999, Copp 1992, Mouton et al. 2012a). Habitats were gently approached by wading and three times 10 randomly selected points were sampled within three different 100 m stretches. Thus, at each location 30 randomly selected points were sampled following the point abundance methodology (Copp 1992). To compensate potential low catch efficiency, each location was additionally sampled for 48h by a fyke of 0.5 x 0.5 x 1 m. Additionally, 4 locations were sampled with fyke nets only (not visualised in Figure 3-12). No juvenile pike were caught with the fyke nets, neither at locations where they were caught by electro fishing.

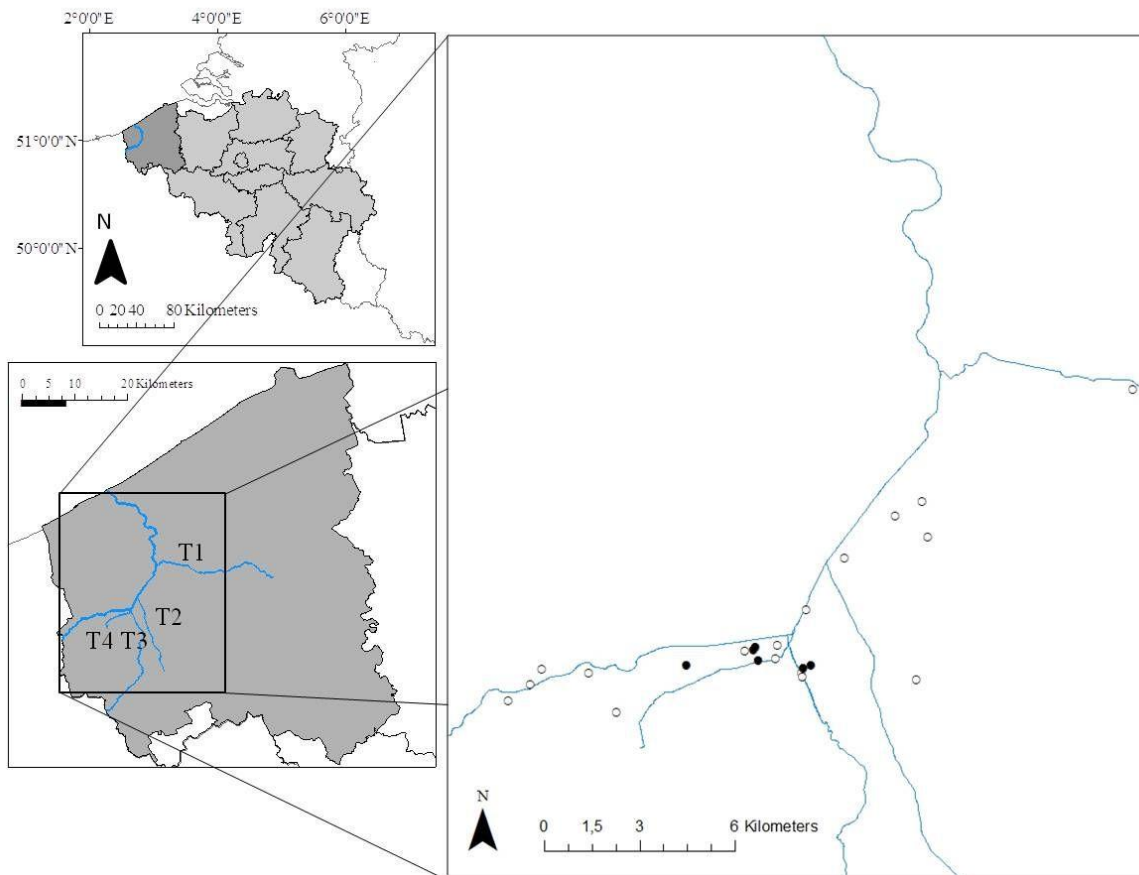


Figure 3-12: Sampling locations of juvenile pike by fyke nets and electrofishing (no YOY caught: white disks and YOY caught: black disks) in the first and second order tributaries and side arms of the river Yser in May and June 2011.

3.5 Data analysis

Data of two pike that were missing before half February and of one pike that was relocated too little were omitted from all analyses (Table 3-3). One (fish ID: 40.661; Table 3-3) of the two pike that were lost before the spawning period lost his tag. The other pike (fish ID: 40.771; Table 3-3) could have been caught by anglers or could have migrated far upstream to spawn. We lost the animal on the 3rd of February 2011. We evaluated if this fish had a different spawning location than the remaining fish during the days following this date by checking all accessible small tributaries, potential spawning grounds and the river Yser in the area till 12 km upstream of the study area. Nonetheless it is possible that we missed this pike. Consequently, the dataset used for the analyses described in chapters 6 and 7 consisted of 813 (755 in winter and spring) pike observations of twelve pike that were each observed between 60 (55 in winter and spring) and 91 (72 in winter and spring) times during the regular tracking campaign (Table 3-3).

Water temperature regimes were used to divide the study period into winter (water temperature below 5°C, November 26th to February 4th) and spring (water temperature between 5 and 15°C, February 5th to April 19th). This division was based on the findings that pike start spawning migration around 5-6 °C (Ovidio & Philippart 2003), spawn at water temperatures between 6 and 14 °C (Raat 1988b) and tend to decrease their activity around 0 °C (Vehanen et al. 2006).

CHAPTER 4

Exploring the opportunities of the CA paradigm for pike migration simulation

4.1 Introduction

This study explores the usability of CAs for spatio-temporal modelling of a pike population to support river management. Specifically, we evaluated the usability of the CA model by analysing its sensitivity to three model parameters: the number of pike in the grid, the initial pike distribution and the grid resolution. Two models were developed that differ in the definition of the neighbourhood and the carrying capacity. In the remainder of this chapter we refer to the models as the basic model and further optimisation of the basic model. The models include habitat characteristics and knowledge on the ecology of pike from published and grey literature, and was tested on a 10 km stretch of the river Yser in Flanders (Belgium). Simulation results showed that the basic model converged to a realistic pike distribution over the study area only at high pike density and low grid resolution, irrespective of the initial pike distribution. Pike density and grid resolution affected the sensitivity to the initial pike distribution in the grid. The sensitivity was smaller but remained after further optimisation of the basic model. Specifically, the sensitivity was high at low pike density and high grid resolution, and absent when pike density was high. This analysis indicated that initial conditions and cell size may have a severe impact on the model output, illustrating the importance of firstly analysing this impact before conducting further analyses.

4.2 Modelling method

4.2.1 Study area and data

We refer to chapter 3 for a detailed description of the study area. For the development of the CA-based model, the study area was divided in cells, each representing 500 and 10 m of the length and the total width of the study area, which is on average 20 m. At both banks of each cell, riparian vegetation and bank structure were assessed visually in the field (Table 3-2). Vegetation was classified into four classes: reed (*Phragmites australis* Cav.), shrubs, scarce

vegetation and no vegetation (INBO, unpublished data). Bank structure was classified into four classes: vertically reinforced banks, tiles, foreshores and semi-natural banks (INBO, unpublished data). River side arms were considered a special bank type and assumed to be particularly suitable as a spawning ground. The assumption was based on knowledge on adult pike ecology and behaviour from A1 publications and books (Bry 1996, Casselman & Lewis 1996, Chapman & Mackay 1984a, b, Craig 1996, Craig 2008, Koed et al. 2006, Vehanen et al. 2006), and grey literature (De Laak & van Emmerik 2006, Inskip 1982). They were therefore assessed differently. Since it is indicated that the hydraulic and physicochemical properties only negligible varied in this study area (Figure 3-8), whereas the spatial variation in the riparian vegetation as well as the degree of disturbance of the river banks was more pronounced, pike habitat suitability was defined based on vegetation and bank structure data. A habitat suitability index was assigned between 0.3 and 1 to each vegetation and bank structure class (Table 4-1). The assignment was based on knowledge on pike ecology and behaviour described in A1 publications, books and grey literature as described above. The HSI of a cell was then calculated as the average of the HSIs along the left and right bank, which were on their turn determined as the average of the HSIs of the vegetation and bank structure. Artificial and natural side arms were considered a particularly suitable habitat for pike and therefore a cell was assigned a HSI of 1 if it contains an artificial or natural side arm. Consequently, the HSI is a ranking (not a quantification) that is derived from knowledge on the effect of vegetation and bank type on pike behaviour from A1 publications, books and grey literature as described above.

Table 4-1: Definition of the Habitat Suitability Index (HSI) of each cell bank in the study area based on the HSIs assigned to the different riparian vegetation and bank structure types. Only combinations of vegetation and bank structure types occurring in the study area were considered. Artificial side arms were considered a particularly suitable habitat for pike and therefore a cell was assigned a HSI of 1 if it contained an artificial side arm.

Vegetation type (HSI)	Bank structure (HSI)	Cell bank HSI
Reed (0.8)	Semi-natural bank (0.8)	0.8
Shrub (0.6)	Semi-natural bank (0.8)	0.7
Reed (0.8)	Foreshores (0.6)	0.7
Shrub (0.6)	Tiles (0.6)	0.6
Scarce vegetation (0.4)	Semi-natural bank (0.8)	0.6
Scarce vegetation (0.4)	Tiles (0.6)	0.5
No vegetation (0.3)	Vertically reinforced bank (0.3)	0.3

Specifically, this approach assumes that pike need shallow places to spawn and vegetation or other plant parts to hide during foraging (Casselman & Lewis 1996, Craig 1996, Craig 2008, Inskip 1982, Meixler et al. 2009). Although other variables like temperature and oxygen concentration may also impact its distribution (Cooper et al. 2008, Inskip 1982, Jacobsen et al. 2007), these variables were not taken into account because their spatial variation in the study area was too limited.

4.2.2 Model structure and assumptions

Characteristic of CAs is the discrete nature of the time, space and state domains. Specifically, a CA consists of an n -dimensional grid of regular or irregular cells c_i that take a certain state s at time step t , i.e. $S(c_i, t)$. The CA grid in this study is 1-dimensional and consists of regular cells that have a state $S(c_i, t)$ which represents the pike abundance in a cell. At each discrete time step this cell state is computed based on specific transition rules, each of them depending on the state of the cell itself and the states of its neighbouring cells c_j (Chen et al. 2011, Wolfram 1983). The neighbouring cells are defined by the neighbourhood, which determines the area that pike can reach in one time step. The basic model and its further optimisation differ in the definition of the neighbourhood.

Basic model

The neighbourhood is confined to the direct left and right neighbour of each cell (Figure 4-1a-e, a-f and a-g), irrespective of the resolution of the grid and the definition of one iteration step. The number of neighbours ($|N(c_i)|$) in the neighborhood function $N: \tau \rightarrow \bigcup_{p=1}^{\infty} \tau^p$ that maps every cell c_i to a finite sequence $N(c_i) = (c_{i_j})_{j=1}^{|N(c_i)|}$, consisting of $|N(c_i)|$ distinct cells c_{i_j} , is thus confined to two. This definition of the neighbourhood does not account for the movement rate of the pike.

Further optimisation of the basic model

In contrast to the basic model, the neighbourhood was defined based on information of the maximal potential distance migrated by an adult pike per iteration step (defined as one day) and the potential presence of a migration barrier. Hence, the neighbourhood was not confined to the direct left and right neighbour, but was extended to the number of left and right neighbours that corresponds with the maximal distance an adult pike can migrate per discrete time step. Different scenarios are depicted in Figure 4-1 to illustrate the difference with a confined neighbourhood and the possibility to integrate a migration barrier. The number of neighbours ($|N(c_i)|$) in the neighborhood function $N: \tau \rightarrow \bigcup_{p=1}^{\infty} \tau^p$ that maps every cell c_i to a finite sequence $N(c_i) = (c_{i_j})_{j=1}^{|N(c_i)|}$, consisting of $|N(c_i)|$ distinct cells c_{i_j} , thus depends on the resolution of the grid (length of the grid cell), the maximal potential distance migrated per time step, the presence of side arms within the maximal potential distance migrated per time step and the potential presence of a migration barrier (Figure 4-1).

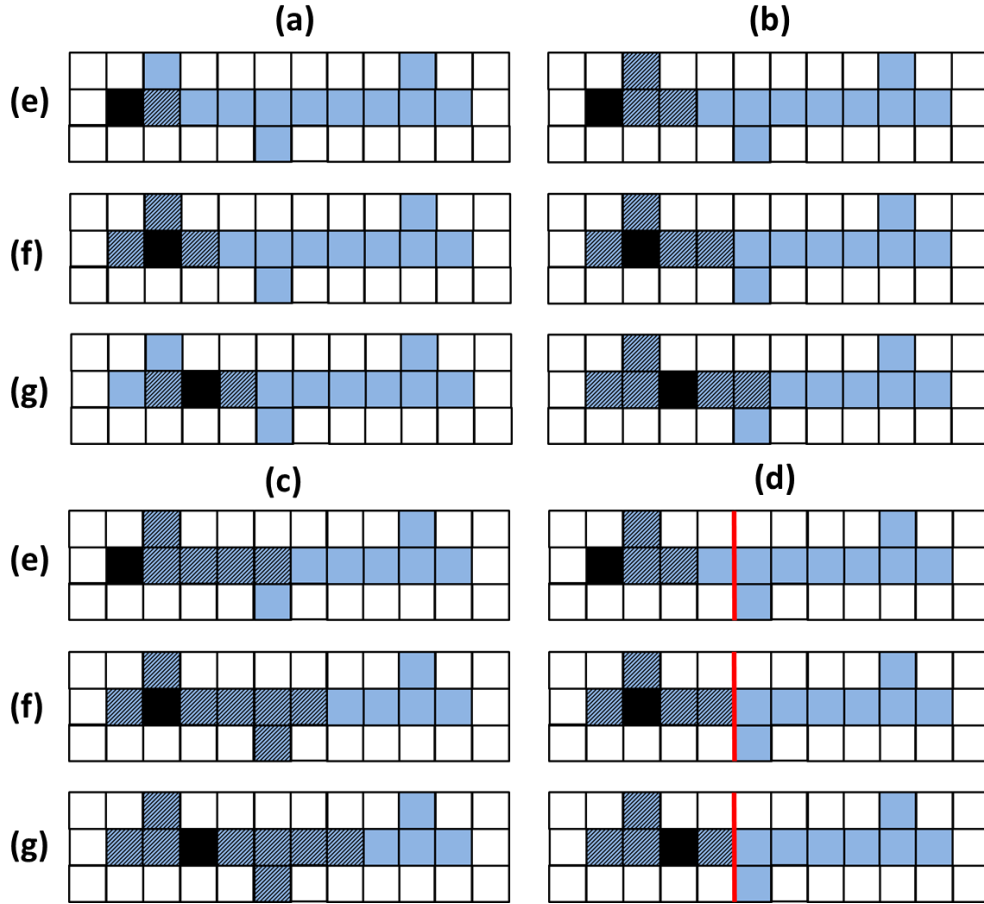


Figure 4-1: Illustration of the neighbourhood (black and blue striped cells) of the first (e), second (f) and third (g) centre cell (black) of a one dimensional grid representing a 5 km long river stretch (blue cells) in four model settings: (a) neighbourhood defined as the direct left and right neighbour of the centre cell, (b) neighbourhood defined as all cells within 1 km of the centre cell, (c) neighbourhood defined as all cells within 2 km of the centre cell and (d) neighbourhood defined as all cells within 2 km of the centre cell and presence of a migration barrier between the fourth and fifth cell of the grid.

The neighbourhood of the optimised model was calculated as follows. First, the distance and degree of adjacency of the cells towards other cells are constant in time and are described by two $N \times N$ matrices, $A_{i,i}$ and $I_{i,i}$, respectively, each having $diag\{0, 0, 0, 0\}$. The first row of each matrix contains the distance and degree of adjacency, respectively, of all cells in the grid towards the first cell of the grid, the second row contains the distance and degree of adjacency, respectively, towards the second cell of the grid and so on. Consequently, assuming a cell length of 10 m in a grid having dimension 1×4 ,

$$A_{i,i} = \begin{bmatrix} 0 & 10 & 20 & 30 \\ 10 & 0 & 10 & 20 \\ 20 & 10 & 0 & 10 \\ 30 & 20 & 10 & 0 \end{bmatrix}$$

and

$$I_{i,i} = \begin{bmatrix} 1 & 2 & 3 & 4 \\ 2 & 1 & 2 & 3 \\ 3 & 2 & 1 & 2 \\ 4 & 3 & 2 & 1 \end{bmatrix}$$

To simulate the effect of one potential migration barrier on adult pike movement, a $2 \times N$ matrix $W_{j,i}$ is described, which indicates the cells that are accessible for pike in each cell of the grid downstream (row $j = 1$ of the matrix) and upstream (row $j = 2$ of the matrix) of the migration barrier. Accessible cells are denoted by 1, whereas inaccessible cells are denoted by 0. Consequently, assuming that a migration barrier occurs at 10 m upstream of the river mouth in a grid with dimensions 1×4 , having cells of 10 m length,

$$W_{j,i} = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 1 \end{bmatrix}.$$

In case no migration barrier occurs, $j = 1$ and

$$W_{j,i} = [1 \quad 1 \quad 1 \quad 1].$$

To account for the movement threshold, a $N \times N$ matrix $X_{i,i}$ is described which indicates the cells that are within pike's movement capacity. The first row of $X_{i,i}$ indicates the cells that are accessible for pike in cell 1 of the grid, the second row indicates the cells that are accessible for pike in cell 2 of the grid, and so on. Consequently, assuming that pike can move 20 m in one time step in a grid with dimensions 1×4 , having cells of 10 m length,

$$X_{i,i} = \begin{bmatrix} 1 & 1 & 0 & 0 \\ 1 & 1 & 1 & 0 \\ 0 & 1 & 1 & 1 \\ 0 & 0 & 1 & 1 \end{bmatrix}.$$

$X_{i,i}$ is calculated by applying the following if-function to each element of matrix $A_{i,i}$:

If the element at the i^{th} row and i^{th} column of matrix $A_{i,i}$ is smaller or equal to the movement threshold
 assign a value of 1 to the element at the i^{th} row and i^{th} column of matrix $X_{i,i}$
else
 assign a value of 0 to the element at the i^{th} row and i^{th} column of matrix $X_{i,i}$
end

The cells that are finally accessible to pike in each cell of the grid, taking into account the position of a potential migration barrier and pike's movement threshold, are described in matrix $Q_{i,i}$. This matrix is determined by multiplying the elements of $W_{j,i}$ with the elements of $X_{i,i}$. If a migration barrier occurs, the elements in row $j = 1$ of $W_{j,i}$ are multiplied with the elements of $X_{i,i}$ in rows $i = 1$ to $i =$ the position of the migration barrier, which is the distance of the migration barrier to the river mouth divided by the cell length, and the elements of row $j = 2$ in $W_{j,i}$ are multiplied with the elements of $X_{i,i}$ in rows $i =$ the position direct upstream of the migration barrier to $i = N$. Consequently, following the example used previously (grid with four cells of 10 m length),

$$Q_{i,i} = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 1 \\ 0 & 0 & 1 & 1 \end{bmatrix}.$$

Matrix $Q_{i,i}$ further controls the redistribution of the pike in each cell of the grid (further named source-cells) by indicating per grid cell (= row in $Q_{i,i}$) to which cells pike may move in the next time step (further named accessible cells).

The presented models are stochastic CAs in which all cells are updated simultaneously by the same transition rules. The impact of the HSI on pike migration is defined by these transition rules (Figure 4-2). The modelled population was assumed to consist only of adults and birth and death processes were not taken into account in the present study.

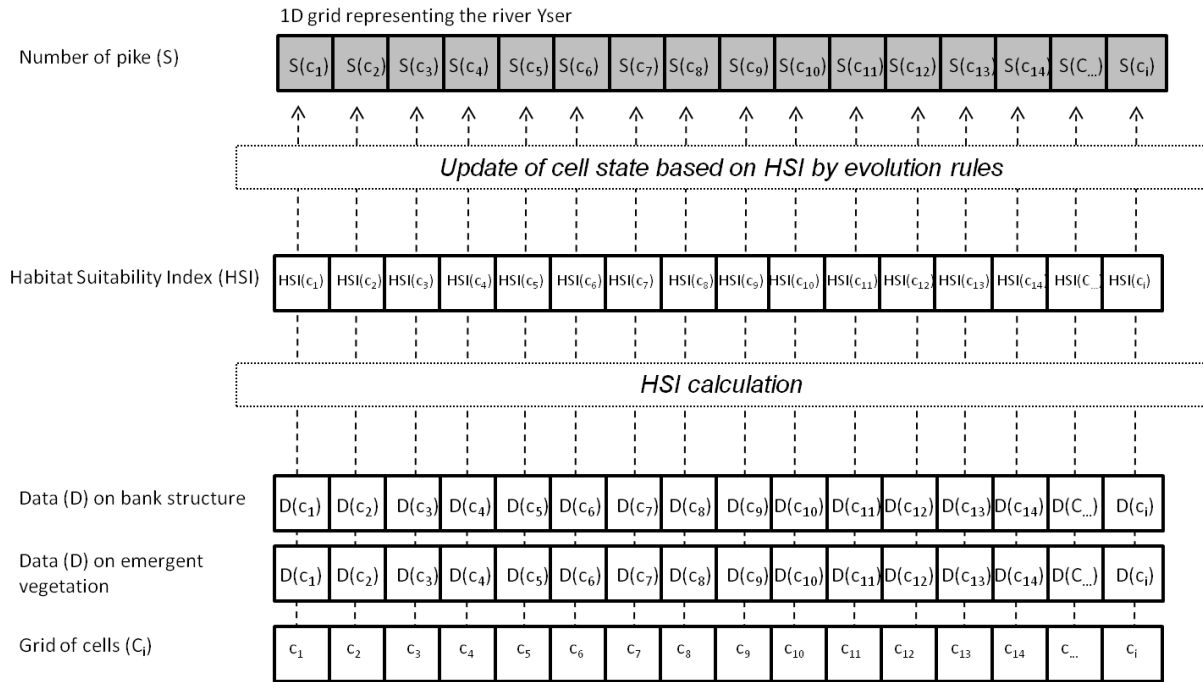


Figure 4-2: Schematic overview of the model structure. Habitat Suitability Index (HSI) calculation was based on vegetation and bank structure data ($D(c_i)$) of each grid cell c_i . The cell state ($S(c_i)$), the number of pike in each cell, was calculated at each time step by transition rules based on the habitat suitability in each cell ($HSI(c_i)$).

4.2.3 Transition rules

The stochastic transition rules (Minss et al. 2000) quantify the number of pike that leave a given cell at each iteration step based on its HSI. The HSIs of the neighbouring cells determine the number of migrating pike that move from c_i to c_j , such that more pike will leave cell c_i if the habitat of c_i is less suitable. Previous research has shown that pike has specific habitat demands (Craig 1996, Craig 2008, Eklöv 1997, Inskip 1982) and that they move to their preferred habitat if possible (Haugen et al. 2006). To integrate random migration and the effect of other variables than habitat suitability, a stochastic component is added to the formula. Specifically, the number of pike in each cell, at a specific time step, is calculated based on its state at the previous time step $t - 1$, $S(c_i, t - 1)$ and on the number of pike that emigrate from or immigrate to that cell $E(c_i, t - 1)$ and $I(c_i, t - 1)$, respectively:

$$S(c_i, t) = S(c_i, t - 1) - E(c_i, t - 1) + I(c_i, t - 1) \quad (4-1)$$

The number of pike $E(c_i, t - 1)$ that emigrate from a cell c_i at time step $t - 1$, is calculated as follows:

$$E(c_i, t - 1) = \lfloor (R(c_i, t - 1)S(c_i, t - 1)((1 - HSI(c_i))(1 - \tilde{E}) + \tilde{E})) \rfloor \quad (4-2)$$

with $HSI(c_i)$ the HSI of cell c_i , \tilde{E} a constant and $R(c_i, t - 1)$ the stochastic component of cell c_i at iteration step $t - 1$. The latter terms ensure that there is always a random fraction of $S(c_i, t - 1)$ that emigrates, irrespective of $HSI(c_i)$. This fraction is quantified by the constant \tilde{E} (which was set to 0.1 in all simulations), and by the stochastic component, $R(c_i, t - 1) \sim U(0.25, 0.5)$ (where U represents a uniform distribution between 25 and 50% of the total number of pike).

Further, the number of pike that immigrated $I(c_i, t - 1)$ to c_i in time step $t - 1$, was calculated as follows:

$$I(c_i, t - 1) = \left\lfloor \sum_{j=1}^{|N(c_i)|} \left(\frac{HSI(c_i)}{\sum_{k=1}^{|N(c_j)|} HSI(c_k)} E(c_j, t - 1) \right) \right\rfloor \quad (4-3)$$

with $E(c_j, t - 1)$ the number of pike leaving the neighbouring cell c_j at time step $t - 1$, and $|N(c_i)|$ and $|N(c_j)|$ being the number of neighbours of respectively c_i and c_j . The modelled population was assumed to consist only of adults and birth and death processes were not taken into account in the present study.

4.2.4 Carrying capacity

Basic model

The basic model does not account for effects of the presence of other pike. Consequently, each cell can contain the total number of pike present in the grid, and a carrying capacity for pike per cell is not included.

Further optimisation of the basic model

Since it is likely that adult pike is a territorial and solitary species (Skov & Koed 2004), it is assumed that a certain habitat or location gets less attractive if other individuals are already present. In the basic model we did not account for this potential effect. Therefore we adapted the model so that a certain carrying capacity per cell is included. This was done by adapting the cell HSI based on the number of pike in the cell. Specifically, when no pike are present, the cell HSI reflects its carrying capacity as the total number of pike that the cell is assumed to be able to sustain. This number is based on the suitability of the cell's habitat, such that suitable habitats may sustain more pike than unsuitable habitats. When pike are present, the HSI is adapted by subtracting the number of present pike from the cell's carrying capacity. The HSI's are updated every iteration step. Consequently, a cell with a high habitat suitability that attracted the maximal sustainable number of pike at iteration step $t - 1$ will not attract any pike at iteration step t , because its suitability lowered to 0..

However, by expressing the cell HSI as a maximal sustainable number of pike, it is possible that the initial number of pike exceeds the carrying capacity of a cell, the study area, or a part of the study area if a migration barrier is present. This is evaluated prior to the simulation by the procedure described below, which redistributes a potential excess number of pike to the nearest neighbouring cells having free space left. If an excess number of pike is present in the study area, this is reported and no further simulations are performed. The procedure also accounts for the maximal potential distance migrated per iteration step.

Procedure: simulation of adult pike migration in a $1 \times N$ grid of cells

N = number of cells in the grid

t = number of iterations, where one iteration is seen as one time step

initialise a vector $\vec{s}_i = (s_1, s_2, \dots, s_N)$, where s_i is the number of pike in cell i

initialise a vector $\vec{h}_i = (h_1, h_2, \dots, h_N)$, where h_i is the habitat suitability in cell i , defined as the maximal sustainable number of pike

initialise a vector $\vec{p}_i = (s_1 - h_1, s_2 - h_2, \dots, s_N - h_N)$; further named **the potential**, which is positive if there are too many pike in the cell and negative if there is place left for pike.

initialise a $t \times N$ matrix $S_{n,i} = \begin{bmatrix} \vec{s}_{1,t} \\ 0 \\ 0 \\ \dots \end{bmatrix}$

initialise a $t \times N$ matrix $P_{n,i} = \begin{bmatrix} \vec{p}_{1,t} \\ 0 \\ 0 \\ \dots \end{bmatrix}$

initialise a $N \times N$ matrix $A_{i,i}$, where the elements denote the distance of each cell to the cells of the grid:

$$A_{i,i} = \begin{bmatrix} 0 & 20 & 40 & 60 \\ 20 & 0 & 20 & 40 \\ 40 & 20 & 0 & 20 \\ 60 & 40 & 20 & 0 \end{bmatrix}$$

initialise a $2 \times N$ matrix $W_{m,i}$, that indicates accessibility of a cell for pike (1: accessible, 0: inaccessible):

$$W = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 1 \end{bmatrix}$$

indicate the position of the barrier as distance to the first grid cell

indicate the maximal distance a pike can move within the predefined time step (T ; named migration threshold)

Start procedure

Calculate a , which is the number of cells that are accessible per grid cell, including the cell itself

initialise a $K \times N$ matrix $T_{k,i}$

initialise a $K \times N$ matrix $K_{k,i}$

$k = 1$

assign p_1 to T_1

assign s_1 to K_1

if the vector at $T_{1,1}$ contains positive values

initialise a new vector \vec{v}_i that contains the positions (i) of the positive values in $T_{1,1}$

initialise a new matrix $M_{i,i}$ that contains in each row i the positions of the cells that are accessible for pike in cell i of the grid, which have a negative potential

select the row of matrix $M_{i,i}$ for which $i = \vec{v}_1$ and define this row as a new vector \vec{m}_i , so that \vec{m}_i contains the positions of the cells where the excessive number of pike (p_i) can access and stay

assign the value of \vec{v}_i to \mathbf{x}

while the length of \vec{v}_i and \vec{m}_i are > 0

 Calculate the position of the cell with a negative potential (out of \vec{m}_i), which is closest to position \mathbf{x}

 If there are two cells with a negative potential at an equal distance of \mathbf{x} , then randomly choose one.

 calculate $K_{k+1,1}$ by putting the excessive number of pike of the cell at position \mathbf{x} at this position

 calculate $T_{k+1,1}$ by subtracting each element of $K_{k+1,1}$ by the corresponding element in \vec{h}_i

 calculate a new vector $\vec{v}\vec{v}_i$ based on $T_{k+1,1}$, which is similar to \vec{v}_i but only contains the positions of the cells with a positive potential that are in the accessible neighbourhood of \mathbf{x}

if the length of $\vec{v}\vec{v}_i$ equals 0

 calculate \vec{v}_i and \vec{m}_i based on $T_{k+1,1}$

 assign the value of \vec{v}_i to \mathbf{x}

else

 make \vec{v}_i equal to $\vec{v}\vec{v}_i$

 calculate \vec{m}_i , but only for the accessible neighbourhood of \mathbf{x}

end

if there are no further negative potentials in $T_{k+1,1}$

 report that there are too many pike in the grid

break

else

if the length of \vec{m}_i equals 0

if $\vec{v}\vec{v}_i > 0$

 report that there are too many pike in the grid

break

else

 reset \mathbf{x} to its first value ever assigned

 assign \mathbf{x} to \vec{v}_i

end

end

end

end

end

End procedure

 assign the last row (which is a $1 \times N$ vector) of $K_{k,i}$ to S_t

 calculate P_t by subtracting each element of \vec{h}_i from S_t

Proceed with the CA-based simulations of migration

4.2.5 Model output and sensitivity analysis

By means of a sensitivity analysis the effect of three model characteristics was analysed: the number of pike in the grid, the initial pike distribution and the grid resolution (Table 4-2). In the **basic model** six simulations were performed in a grid with 20 cells of 500m long (a coarse grid; C), and six in a grid having 1000 cells of 10 m in length (a fine grid; F). In the **further optimisation of the basic model** six simulations were performed in the coarse grid and no simulations were performed in the fine grid. Each of the simulations differed in pike grid density and in the initial distribution, which was even (E) or uneven (U). At an even distribution every cell of the grid contains an equal number of pike, whereas at an uneven distribution only the first cell contains all the pike. Three different grid densities of pike were tested: 20 (L), 200 (M) and 1200 (H) pike.grid cell⁻¹ (Table 4-2). The tested densities were based on three different field observations of carrying capacity: 2.3-8.3 adults.ha⁻¹ by Craig (1996), 40-50 adults.ha⁻¹ and 1.1-1.6 adults.ha⁻¹ by Margenau et al.(2008). The simulations are identified with a three-letter code, in which the first letter indicates the grid type (C or F), the second indicates the pike density (L, M or H) and the last indicates the initial distribution (E or U) (Table 4-2). Furthermore, in every simulation the side arms were empty at the first iteration step.

The different simulations were compared based on the number of iterations before model convergence (A) and on the final pike distribution obtained after convergence (B).

(A) was assessed by measuring the net migration, which was defined as the total change in number of pike of all grid cells between two consecutive iteration steps. At model convergence the net migration fluctuates around a steady-state value and no longer affects the pike distribution across the study area.

(B) was analysed based on three different approaches: the pike distribution over the different HSI values in the study area, the pike distribution across the study area and the Shannon-Wiener entropy of the pike distributions across the study area, H (Shannon 1948). The analysis of the first two entailed a comparison of the distributions with the assumed pike distribution across the study area. The assumed distribution was calculated as the product of the total number of pike and the likelihood that a pike individual would end up in a certain cell, which is the product of the HSI class and the frequency of its occurrences, scaled between 0 and 1 in the basic model and between 0 and the total number of pike in the grid in the further optimisation of the basic model. Consequently, pike are not necessarily most likely to end up in the side arms, although these have the highest HSI (Figure 4-3B and D, and Figure 4-4).

The third approach, the Shannon-Wiener entropy H , calculates the entropy as follows:

$$H = - \sum_{i=1}^P \frac{n_i}{N} \log\left(\frac{n_i}{N}\right) \quad (4-4)$$

where P is the number of cells, N is the total number of pike in the grid and n_i is the number of pike per cell. For every iteration step, H can be calculated and compared to the assumed H (Figure 4-6 to Figure 4-17D). All analyses were performed in Mathematica (<http://www.wolfram.com/mathematica>).

Table 4-2: Overview of the 12 simulations evaluating the sensitivity of the model output to the total number of pike in the grid, initial pike distribution over the study area and grid resolution. The results of simulations FL and FM were not presented, because they were similar to simulations CL and CM.

Cell length (representing length (m))	Number of pike in the grid (# pike·grid ⁻¹)	Initial pike distribution (initial H)	Code	Result
500	20	Evenly distributed	CLE	Figure 4-6; Figure 4-14
500	20	All initially in one cell	CLU	Figure 4-7; Figure 4-15
500	200	Evenly distributed	CME	Figure 4-8; Figure 4-16
500	200	All initially in one cell	CMU	Figure 4-9; Figure 4-17
500	1200	Evenly distributed	CHE	Figure 4-10
500	1200	All initially in one cell	CHU	Figure 4-11
10	1000	All initially in one cell	FLE	Not shown
10	1000	Evenly distributed	FLU	Not shown
10	10000	All initially in one cell	FME	Not shown
10	10000	Evenly distributed	FMU	Not shown
10	60000	Evenly distributed	FHE	Figure 4-12
10	60000	All initially in one cell	FHU	Figure 4-13

4.3 Results basic model

4.3.1 Steady-state pike distribution

Distribution across the study area

The results showed a strong impact of the grid resolution and the pike density on the final pike distribution, whereas a weaker effect of the initial pike distribution was observed (Figure 4-5). Specifically, the CHE and CHU simulations led to similar pike distributions and showed close agreement with the assumed distribution over the study area (Figure 4-3A, Figure 4-5, Figure 4-8A, Figure 4-9A) in contrast to other simulations. For the L simulations, migration did not occur when the initial distribution was even (CLE and FLE) and was restricted to the neighbourhood of the initially occupied cell in simulations where the initial distribution was uneven (CLU and FLU; Figure 4-7 and Figure 4-8A respectively). Although the steady-state pike distribution in the CME simulations did not reflect the assumed pike distribution, pike already preferred the side arms and the high-quality habitats in the river over the low-quality habitats. In contrast, in the CMU simulations the high-quality habitats upstream were not occupied (Figure 4-9A). A similar impact of the initial pike distribution was observed in the FM and FH simulations, although in contrast to the CME simulation, the high-quality habitats

were not preferred over the low-quality habitats in the FME simulation. The FL and FM simulation results were not presented, because they were similar to the CL and CM simulations.

Entropy

Only in the CHE, CHU and CMU simulations the final entropy differed less than 1.2 from the assumed entropy (Figure 4-9, Figure 4-10 and Figure 4-11D). The smallest difference (0.2) was observed in the simulation that did not lead to the assumed distribution (CMU; Figure 4-5 and Figure 4-9), emphasizing the need to consider not only the entropy but also the spatial pike distribution to evaluate model performance. Additionally, the difference between the resulting and assumed entropy was higher in F simulations, compared to C simulations and lower in U simulations compared to E simulations, except for simulations CHE and CHU, which did not differ (Figure 4-10 and Figure 4-11). Overall, simulation results showed a smaller influence of initial pike distribution at higher pike densities (Figure 4-7 and Figure 4-8).

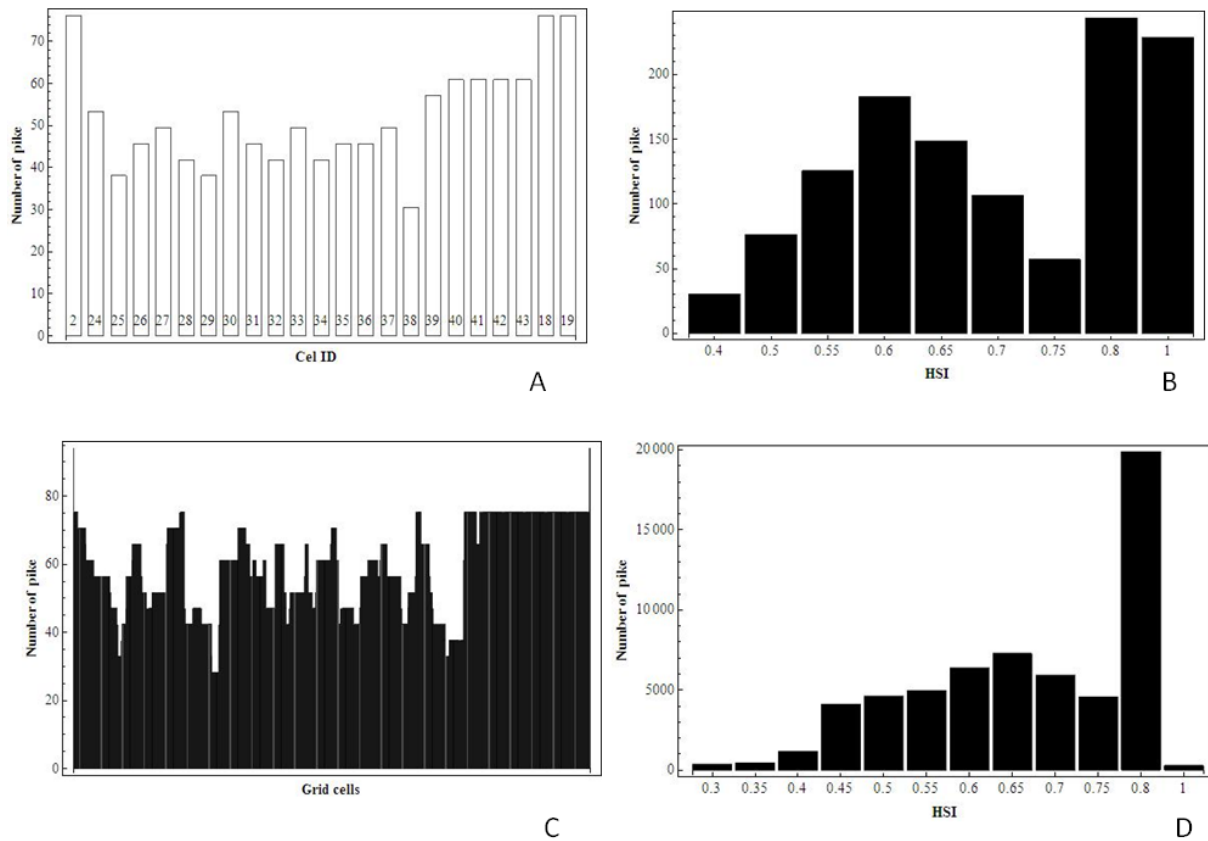


Figure 4-3: Assumed distributions of pike over the whole grid (A) and over the HSI classes (B) in the grid with cell lengths representing 500 m, and over the whole grid (C) and over the HSI classes (D) in the grid with cell lengths representing 10 m.

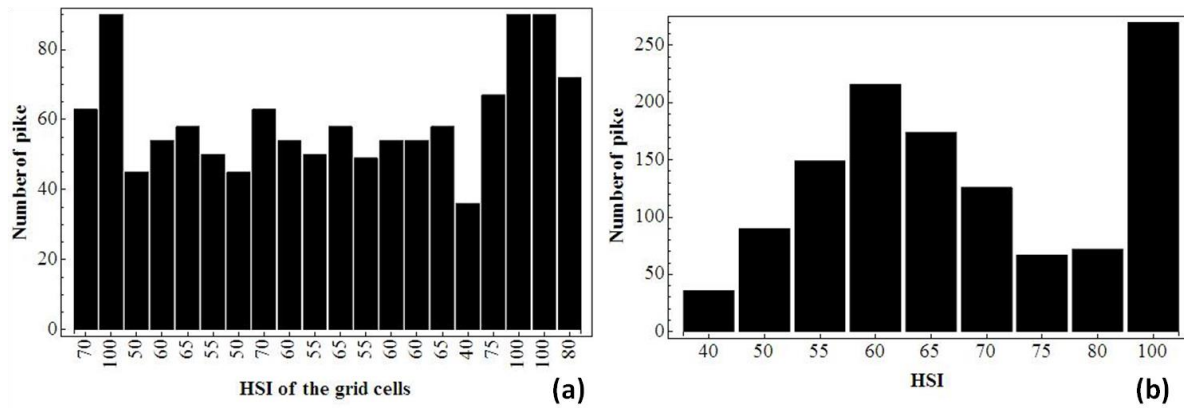


Figure 4-4: Assumed distributions of pike over the whole grid (a) and over the HSI classes (b) in the grid with cell lengths representing 500 m. The total number of pike distributed over the grid and HSIs is 1200, according to the maximal numbers of pike evaluated (Table 4-2).

HSI distribution

The pike distribution across the HSIs showed close agreement with the assumed distribution for simulations with a high pike density, such as the CHE, CHU and FHE simulations, but not in the FHU simulation. Although the CM and FM simulations did not lead to an assumed pike distribution, their distribution across the HSIs did approximate the assumed HSI distribution when pike were initially evenly distributed (CME and FME) (Figure 4-8B).

4.3.2 Number of iteration steps before convergence

The number of iteration steps needed to obtain convergence was affected by the number of pike in the grid, the initial pike distribution and the grid resolution. At high grid resolution (F simulations), more iteration steps were needed in the E than U simulations, whereas a course resolution required less iteration steps in the E than U simulations (Figure 4-5). For those simulations that led to the assumed pike distribution and entropy, 1200 (CHE) and 3400 (CHU) iteration steps were needed before convergence was reached (Figure 4-3, Figure 4-10 and Figure 4-11C), whereas C simulations with a lower pike density (CL and CM) showed faster convergence. By comparison, the maximum number of iteration steps needed to reach convergence in the F simulations was only 10 000, although the grid resolution was 50 times higher than in the C simulations. This indicates that convergence was reached in the former, before the assumed pike distribution was obtained, which was confirmed by our previous results. For instance, the FME and FLU simulations already reached convergence after 6000 and 2000 iteration steps, respectively, and the FMU and FHU simulations already after 100 iteration steps (Figure 4-5), but none of these simulations led to the assumed pike distribution. At low pike density no net migration occurred (simulations CLE, CLU and FLE; Figure 4-5).

Study area distribution	HSI distribution		
Iteration steps	Entropy		
-	-	-	±
1	-	100	-
		1200	+
		CLE CME CHE	
-	-	-	-
1	-	3000	+
		3400	+
		CLU CMU CHU	
-	-	-	+
1	-	2000	-
		10000	-
		FLE FME FHE	
-	-	-	-
6000	-	100	-
		100	±
		FLU FMU FHU	

Figure 4-5: Schematic overview of the simulation performances by good (+), moderate (±) or poor (-) ability to approximate the assumed distribution over the study area (study area distribution, top left), over the HSIs (HSI distribution, top right) and entropy (bottom right), and the number of iteration steps needed before convergence (bottom left). The codes identify the simulation parameters: C: coarse grid, F: fine grid, L: low pike density (1 pike.cell-1), M: medium pike density (10 pike.cell-1), H: high pike density (60 pike.cell-1), E: pike initially evenly distributed and U: pike initially not evenly distributed.

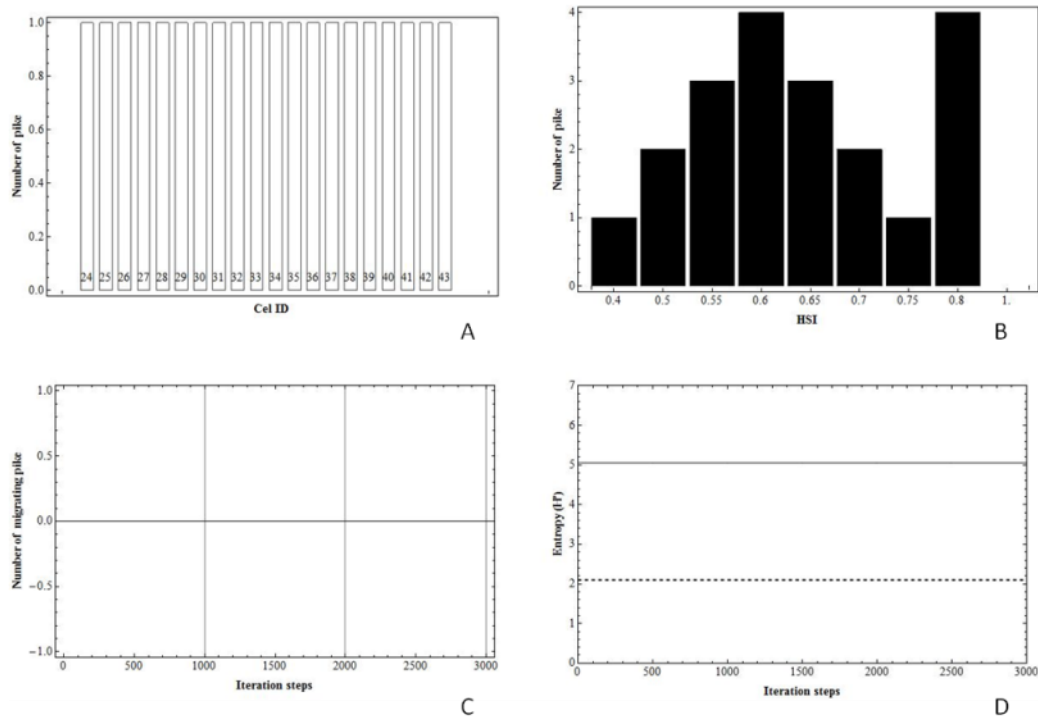


Figure 4-6: Output of the CLE simulation showing the pike distribution over the study area (A), the number of pike per Habitat Suitability Index (HSI) value (B), the number of pike migrating between two consecutive time steps (averaged over ten consecutive time steps, C) and the entropy H of the pike distribution over the study area (D). The dashed line indicates the assumed H .

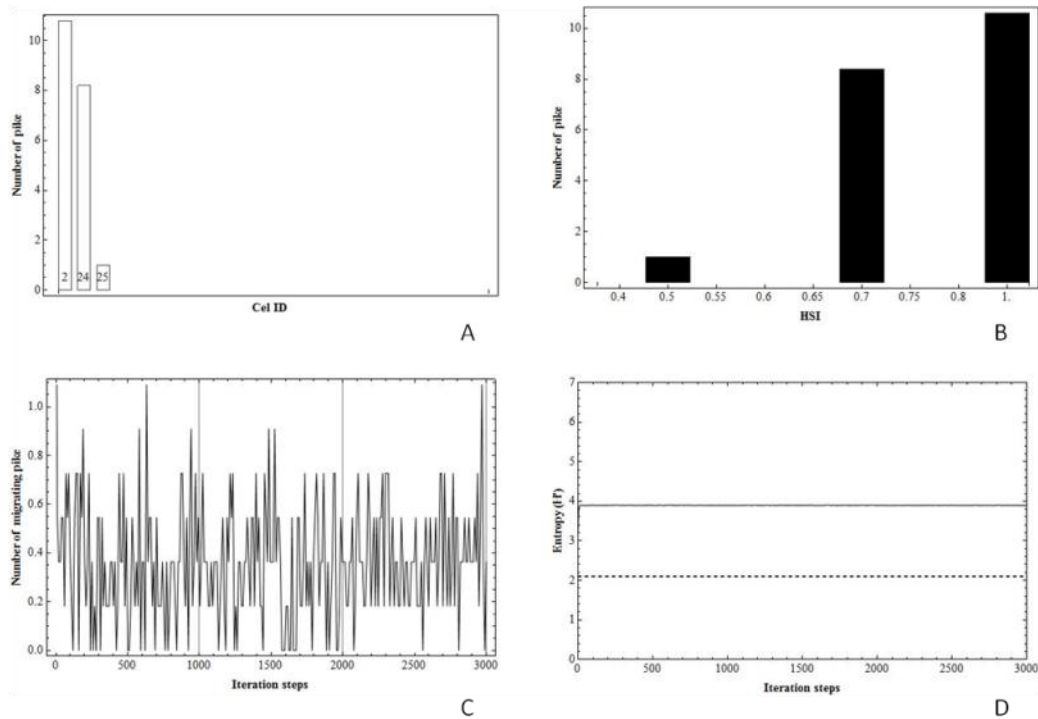


Figure 4-7: Output of the CLU simulation showing the pike distribution over the study area (A), the number of pike per Habitat Suitability Index (HSI) value (B), the number of pike migrating between two consecutive time steps (averaged over ten consecutive time steps, C) and the entropy H of the pike distribution over the study area (D). The dashed line indicates the assumed H .

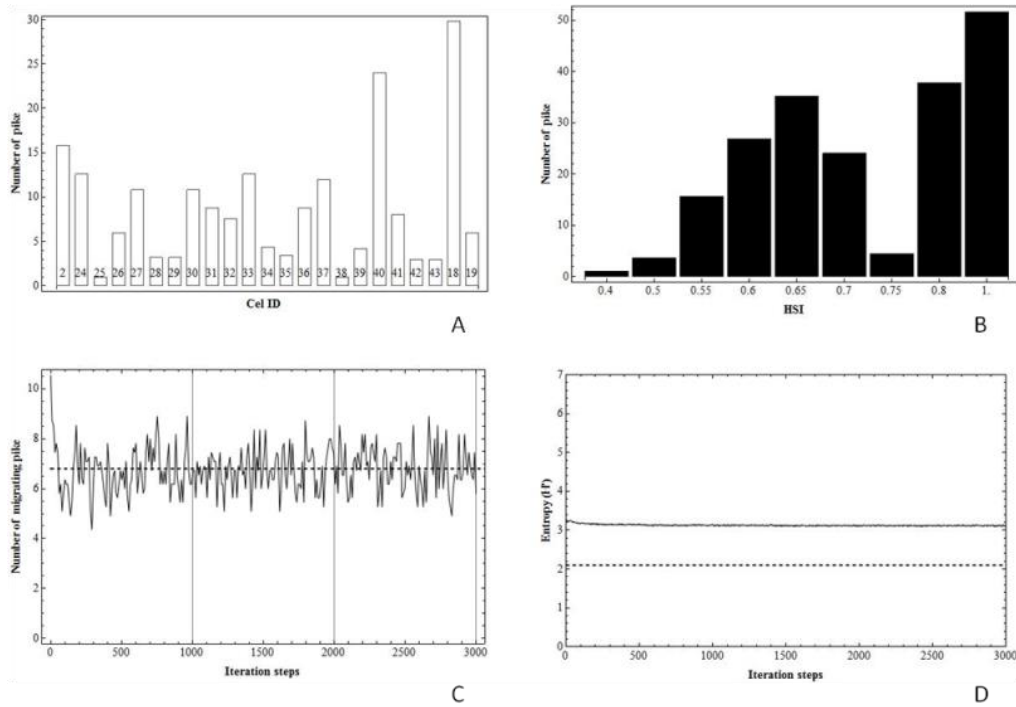


Figure 4-8: Output of the CME simulation showing the pike distribution over the study area (A), the number of pike per Habitat Suitability Index (HSI) value (B), the number of pike migrating between two consecutive time steps (averaged over ten consecutive time steps, C) and the entropy H of the pike distribution over the study area (D). The dashed line indicates the assumed H .

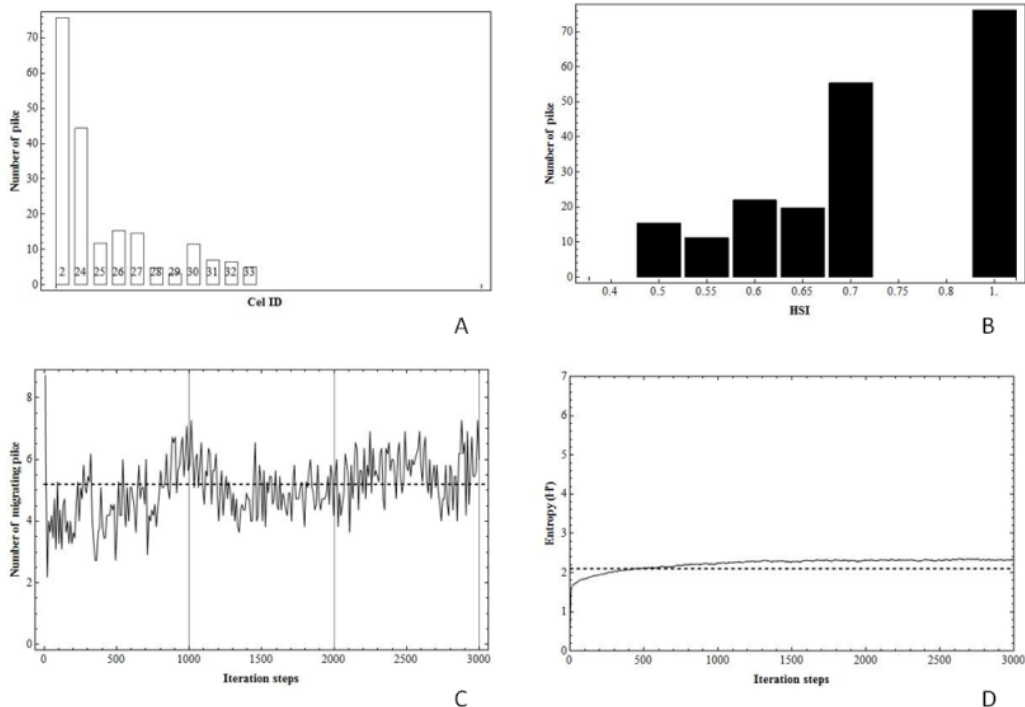


Figure 4-9: Output of the CMU simulation showing the pike distribution over the study area (A), the number of pike per Habitat Suitability Index (HSI) value (B), the number of pike migrating between two consecutive time steps (averaged over ten consecutive time steps, C) and the entropy H of the pike distribution over the study area (D). The dashed line indicates the assumed H .

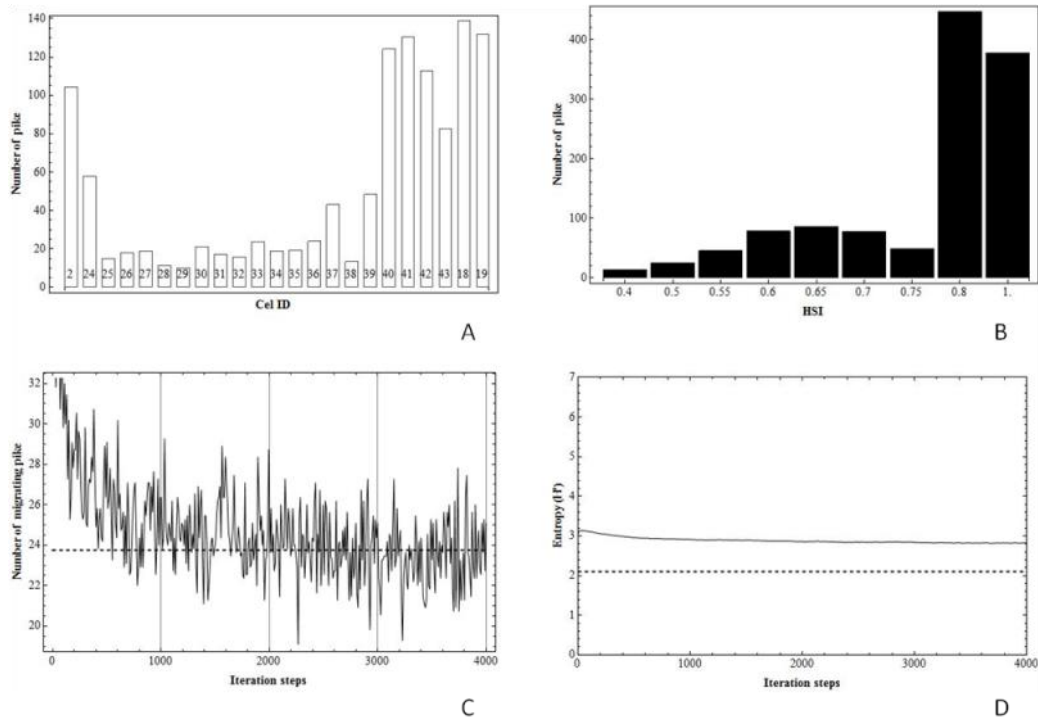


Figure 4-10: Output of the CHE simulation showing the pike distribution over the study area (A), the number of pike per Habitat Suitability Index (HSI) value (B), the number of pike migrating between two consecutive time steps (averaged over ten consecutive time steps, C) and the entropy H of the pike distribution over the study area (D). The dashed line indicates the assumed H .

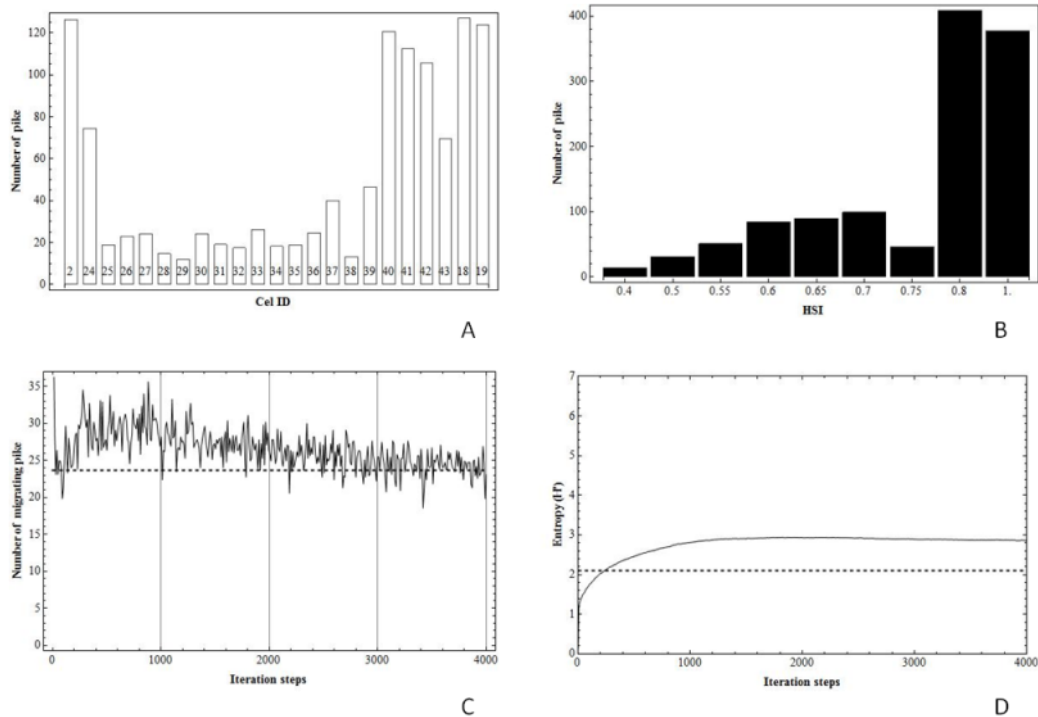


Figure 4-11: Output of the CHU simulation showing the pike distribution over the study area (A), the number of pike per Habitat Suitability Index (HSI) value (B), the number of pike migrating between two consecutive time steps (averaged over ten consecutive time steps, C) and the entropy H of the pike distribution over the study area (D). The dashed line indicates the assumed H .

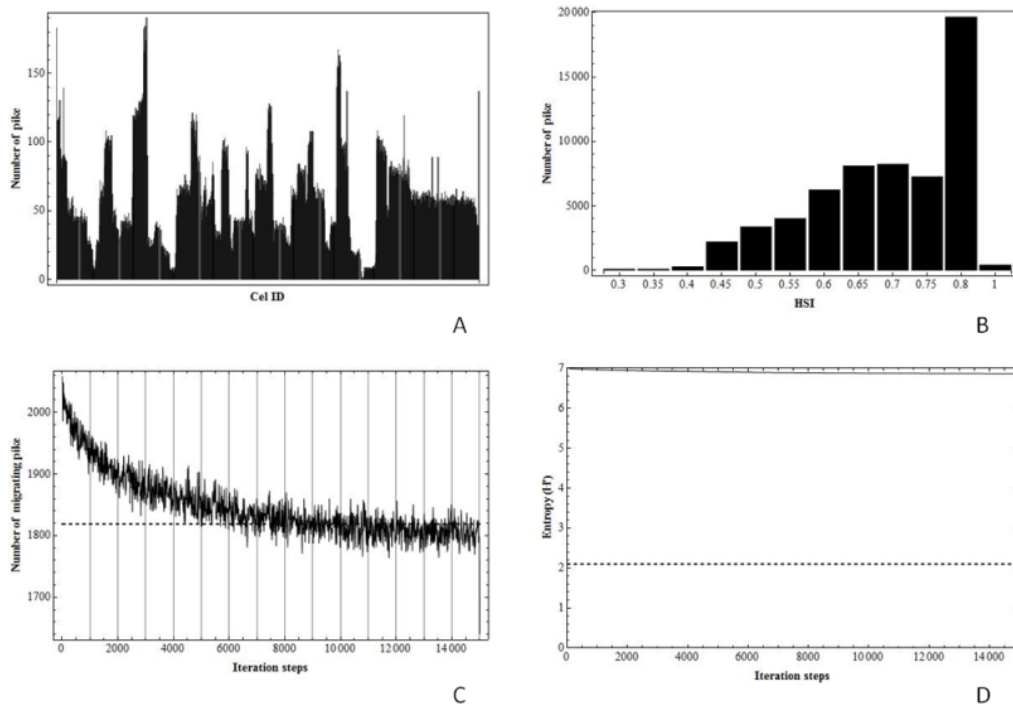


Figure 4-12: Output of the FHE simulation showing the pike distribution over the study area (A), the number of pike per Habitat Suitability Index (HSI) value (B), the number of pike migrating between two consecutive time steps (averaged over ten consecutive time steps, C) and the entropy H of the pike distribution over the study area (D). The dashed line indicates the assumed H .

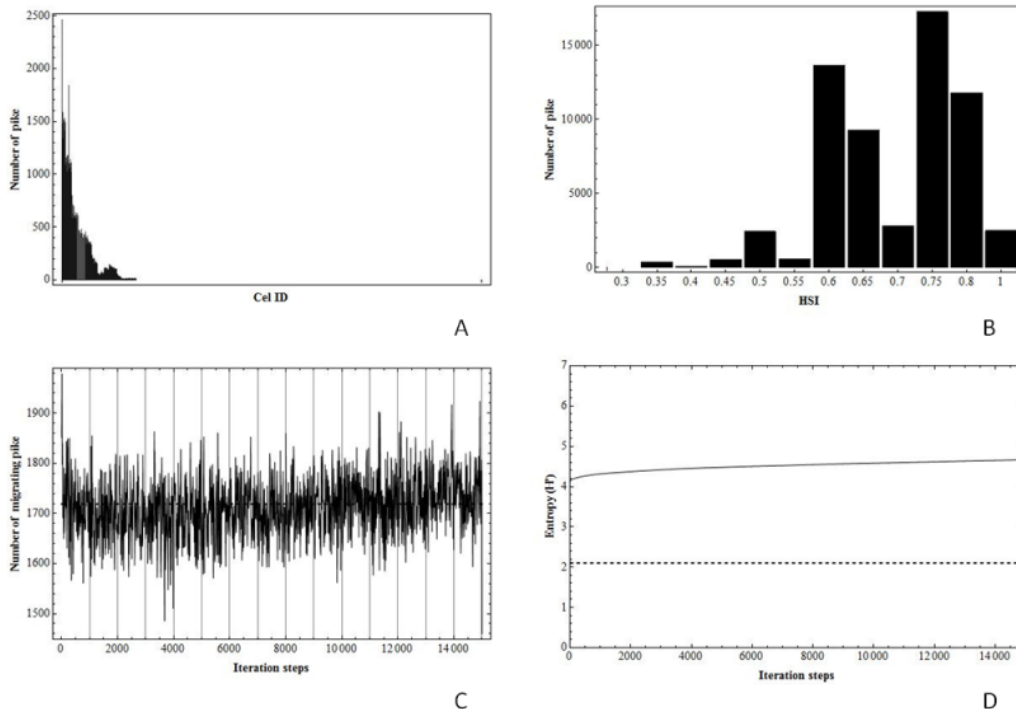


Figure 4-13: Output of the FHU simulation showing the pike distribution over the study area (A), the number of pike per Habitat Suitability Index (HSI) value (B), the number of pike migrating between two consecutive time steps (averaged over ten consecutive time steps, C) and the entropy of the pike distribution over the study area (D). The dashed line indicates the assumed H .

4.4 Results further optimisation of the basic model

4.4.1 Steady-state pike distribution

Distribution across the study area

The results showed an effect of the number of pike in the grid, whereas a weaker effect of the initial pike distribution was observed (Figure 4-14 to Figure 4-17). Specifically, the procedure to check a potential excess of pike versus the carrying capacity revealed that the numbers tested in the CHE and CHU simulations were exceeding the carrying capacity of the study area. For the L simulations, migration did not occur when the initial distribution was even (CLE) and was restricted to the first half of the study area where the initial distribution was uneven (CLU; Figure 4-14 and Figure 4-15A respectively). The steady-state pike distribution in the CME simulations did reflect the assumed pike distribution not perfectly, but better than in the basic model. Specifically, the distribution over the grid, evaluated by the entropy, was matching the expectations well. Pike preferred the spawning places and the high-quality habitats in the river over the low-quality habitats and the median quality habitats that were relatively more available also contained a higher total number of pike. The results of the CMU simulations were similar to the CME simulations. Although all high-quality habitats were occupied in the CME and CMU simulations, the distribution of the pike over the high quality habitats was not equal (Figure 4-16 and Figure 4-17A). The variation in the final number of pike per grid cell in the CME and CMU simulations did not differ much between all five repetitions per simulation, which indicates a robust final output (Figure 4-18).

Entropy

Only in the CME and CMU simulations the final observed entropy (0.4) differed little from the assumed entropy (Figure 4-16 and Figure 4-17D). The entropy for simulations CHE and CHU was not evaluated, since the tested pike density was exceeding the carrying capacity of the study area. In contrast to the results for the CME and CMU simulations in the basic model, the entropy is equal in the optimisation of the CA-based model and the initial pike distribution had thus no impact on the resulting entropy. However, the difference in observed and assumed entropy of the CMU simulation in the basic model was smaller than the difference found for the optimisation of the CA presented here (0.2 versus 0.4, respectively).

HSI distribution

The pike distribution across the HSIs showed agreement with the assumed distribution for simulations CME and CMU (Figure 4-16 and Figure 4-17A), but not for simulations CLE and CLU (Figure 4-14 and Figure 4-15A). The difference in the pike distribution over the HSI's of simulation CME were the number of pike in cells having a HSI of 80. Relatively too many pike occur in those cells compared to cells having the best (100) HSI. Further, relatively too little pike occurred in the cells having a HSI of 40 to 50 and 70 to 75 compared to the median quality cells (HSI's of 55 to 65; Figure 4-16B). The difference between the assumed pike distribution over the HSI' and the one observed in the CMU simulation was less big and specifically the cells having a HSI of 80 contained too many pike compared to the cells with the most suitable habitat (Figure 4-17B).

4.4.2 Number of iteration steps before convergence

The number of iteration steps needed to obtain convergence was not affected by the initial pike distribution, but was affected by the number of pike in the grid. Although there was a difference between the E and U simulation for low pike density (CLE and CLU), there was no difference in the medium pike density simulations (CME and CMU). For the best performing

simulations (CME and CMU), around 600 iteration steps were needed before convergence was reached (Figure 4-16 and Figure 4-17C). By comparison, this is about 1400 and 3400 iteration steps faster than the CME and CMU simulations in the basic model, respectively.

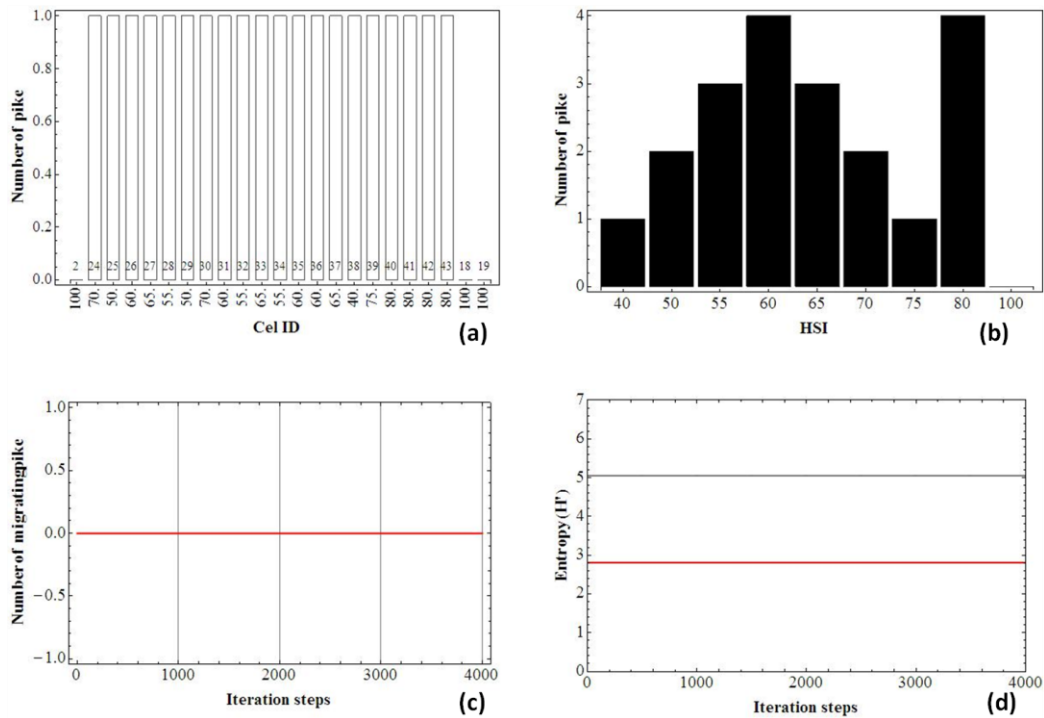


Figure 4-14: Output of the CLE simulation showing the pike distribution over the study area (a), the number of pike per Habitat Suitability Index (HSI) value (b), the number of pike migrating between two consecutive time steps (c) and the entropy H of the pike distribution over the study area (d). The red line indicates the assumed H .

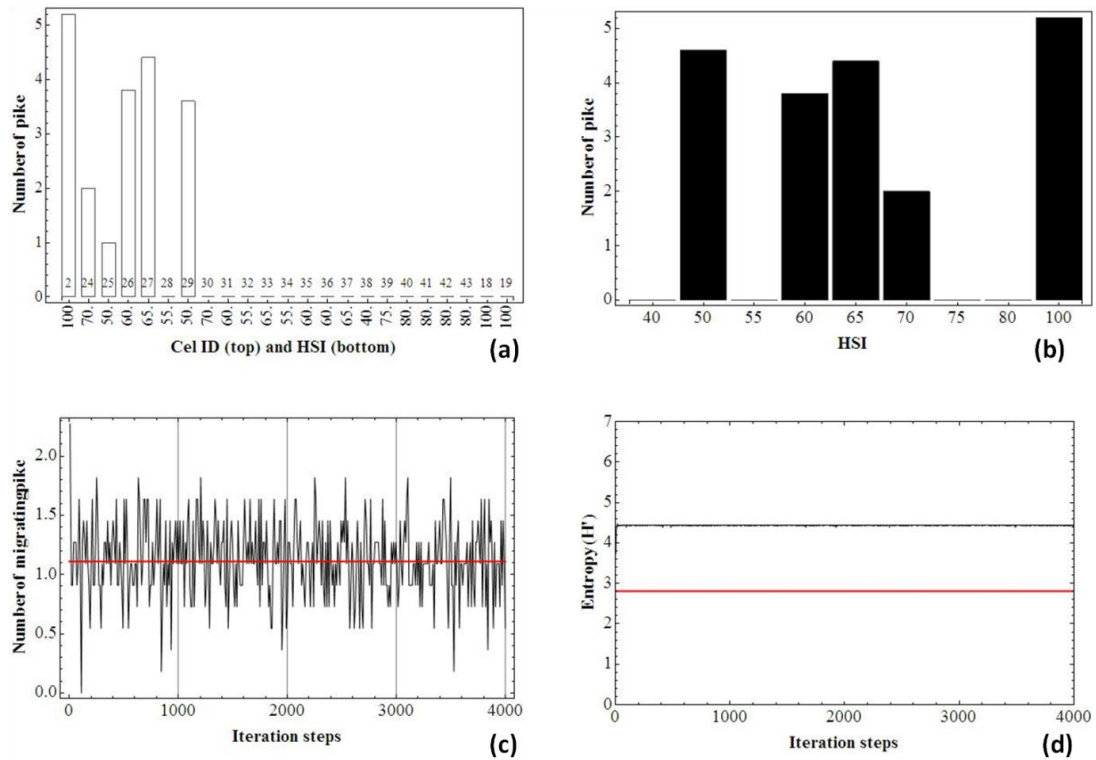


Figure 4-15: Output of the CLU simulation showing the pike distribution over the study area (a), the number of pike per Habitat Suitability Index (HSI) value (b), the number of pike migrating between two consecutive time steps (c) and the entropy H of the pike distribution over the study area (d). The red line indicates the assumed H .

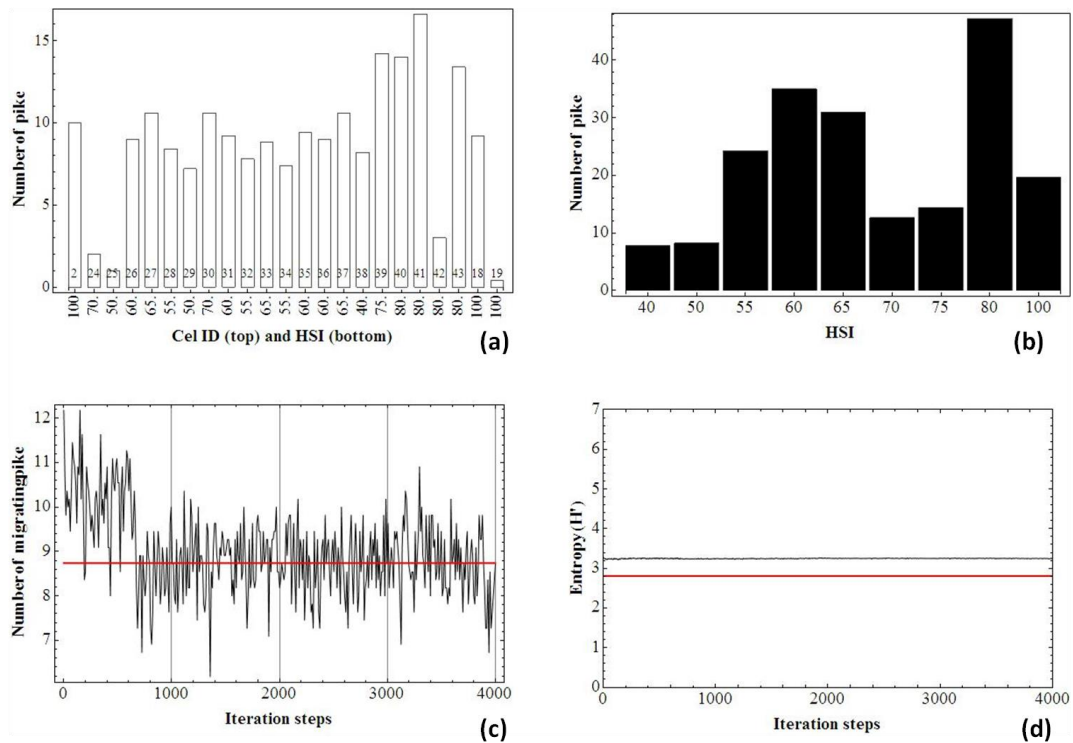


Figure 4-16: Output of the CME simulation showing the pike distribution over the study area (a), the number of pike per Habitat Suitability Index (HSI) value (b), the number of pike migrating between two consecutive time steps (c) and the entropy H of the pike distribution over the study area (d). The red line indicates the assumed H .

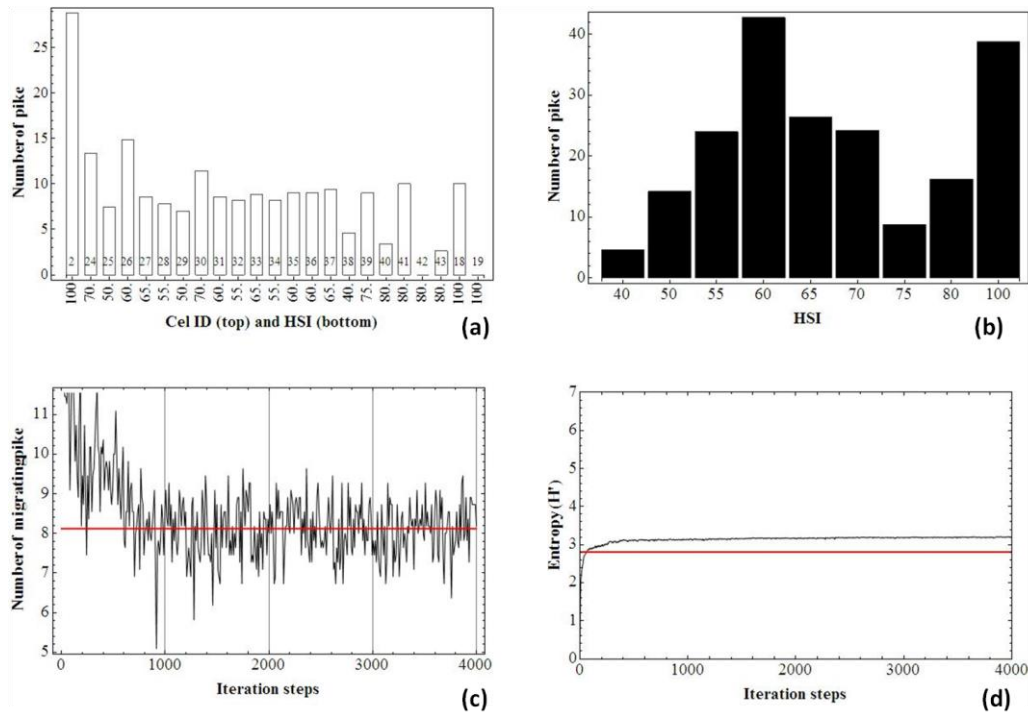


Figure 4-17: Output of the CMU simulation showing the pike distribution over the study area (a), the number of pike per Habitat Suitability Index (HSI) value (b), the number of pike migrating between two consecutive time steps (c) and the entropy H of the pike distribution over the study area (d). The red line indicates the assumed H .

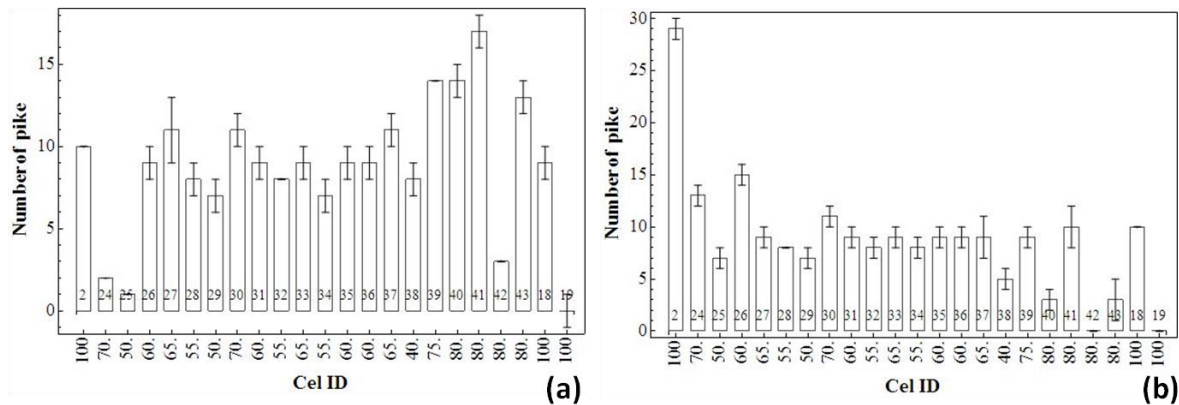


Figure 4-18: Average and standard deviation of the number of pike per grid cell in the last iteration step (of 4000 iteration steps) of five repetitions of the CMU simulation.

4.4.3 Scenarios

The results of the first scenario differ from the results of simulation CMU, although the only difference between the two simulations is the migration threshold of 2000 m per iteration step. The pike do not reach the upstream part of the grid and it takes about 2000 iteration steps before the model converges (Figure 4-19A and C). In the second scenario the model converges from the first iteration steps onwards and pike do not reach the habitats upstream of the migration barrier (Figure 4-19B and D).

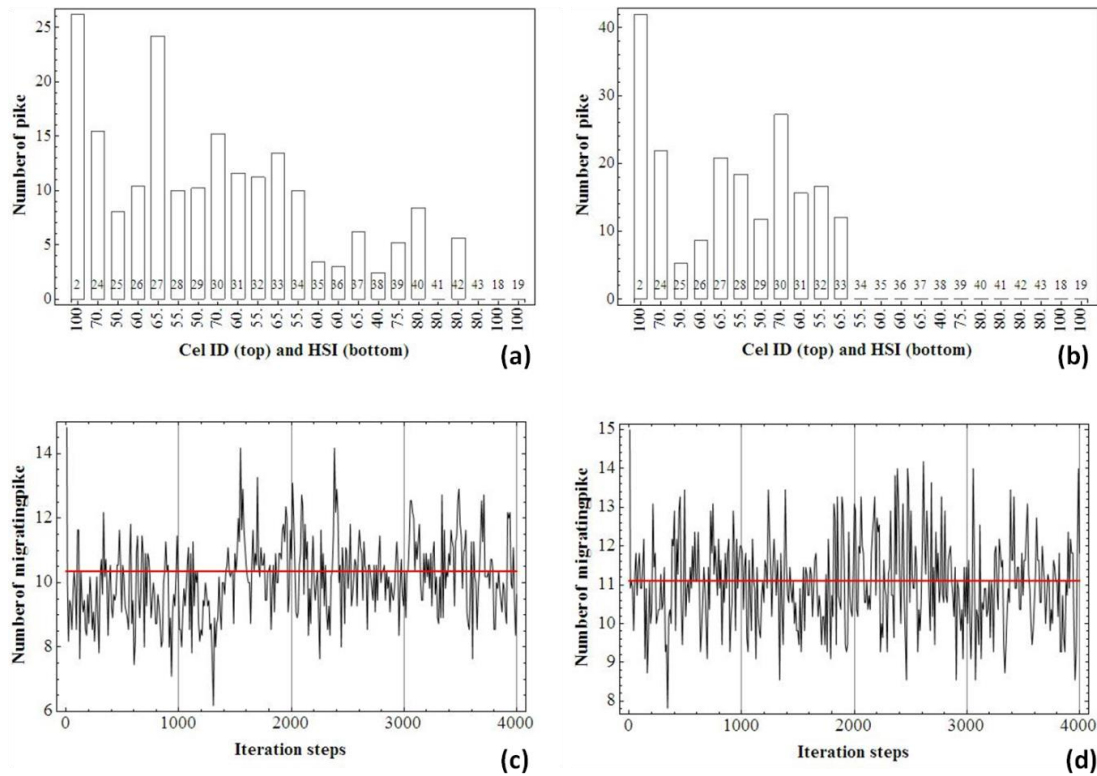


Figure 4-19: Output of two simulations of 200 pike in a coarse grid (C simulations) in the absence of a migration barrier and with a migration threshold of 2000 m (a and c), and in the presence of a migration barrier at 5000 m upstream without a migration threshold (b and d). a and b: distribution of the pike over the grid after 4000 iteration steps, c and d: number of migrating pike per iteration step.

4.5 Discussion

In the **basic model** we examined in 12 simulations the effect of the number of pike in the grid, the initial pike distribution and the grid resolution. The mutually divergent outcomes of these simulations strongly indicate the sensitivity of the model to the number of pike in the grid and to the grid resolution. The results of the CH simulations showed closest agreement with the assumed pike distribution. A possible explanation may be that these simulations possess an optimal trade-off between the number of pike in the grid and the grid resolution. In other simulations, the model may converge because the cell densities decline to one, whereas in the CH simulations, convergence only occurs because the assumed pike distribution is reached. Specifically, the results of the CLE simulation indicate that migration is prevented by densities of one in subsequent cells. Consequently, in this case migration stabilizes before the assumed distribution is reached. The likelihood that cell densities equal one is higher at low initial pike densities and high grid resolutions. Additionally, it is also interesting to note that although the pike densities are equal for CH and FH simulations, the latter did not lead to an assumed pike distribution. A plausible explanation may be that at a higher resolution, clusters of cells with a similar HSI are more likely to occur. The transition rules are not adequate to simulate migration through such clusters and lead to a net migration that is zero or completely random. This is an interesting finding that supports the view of Chen and Mynett (2003), who state that it is important, but also difficult to couple the different physical and ecological scales of an ecosystem spatially and temporally.

The same was concluded after **further optimisation of the basic model** by a larger neighbourhood and inclusion of a carrying capacity per cell. By six simulations in a coarse

grid (cells representing 500 m of river length) we evaluated whether these adaptations reduce the sensitivity of the CA-based model to the total number of pike in the grid and the initial distribution of the pike in the grid. In contrast to the basic model, this was not evaluated in a fine resolution grid (cells representing 10 m of river length), since the tests of the basic model indicated a worse performance of the model at this resolution. However, it would be interesting to evaluate the applicability of the optimised model in the fine grid in future, after the CA works properly in the coarse grid. Specifically, the results indicated that even after extension of the neighbourhood and inclusion of a carrying capacity per cell, the model is still sensitive to the total number of pike in the grid. However, the sensitivity is smaller. Specifically, the CM simulations showed closer agreement with the assumed distribution and less iteration steps were necessary to obtain convergence. Further, the results suggest absence of sensitivity to the initial pike distribution. The outcome of the CLE simulation was similar to that of the basic model and migration was prevented by densities of one in subsequent cells. Hence, migration stabilized before the assumed distribution was reached. The likelihood that cell densities equal one is higher at low initial pike densities or a high grid resolution in which case the carrying capacity per cell is lower.

Consequently, the results show that the optimisation of the CA-based model is still directly sensitive to the total number of pike in the grid, and indirectly via the trade-off between the grid resolution and the pike density. Nonetheless, the adaptation of the neighbourhood and the HSI definition have increased the range of optimal trade-offs between pike density and grid resolution and have lowered the constraints posed on the temporal aspect of migration as indicated by the better results of the CM simulations. However, these results still suggests that to improve the applicability of the model for low pike densities the transition rules need to be adapted. Future research on the transition rules is desirable to enhance the applicability of the model for low pike densities.

The preliminary test of the scenarios indicate that the adaptations now allow to evaluate an excess number of pike in the grid, the existence of a migration threshold and the presence of a potential migration barrier. However, to really evaluate whether these adaptations led to an improved reliability of the model, the model sensitivity should first be tackled by further research on the transition rules.

Overall, the results clearly illustrate an impact of the model settings on the simulation outcome and consequently indicate the importance of choosing the appropriate settings, which is in line with the findings of Chen and Mynett (1999) and Li (2009). Additionally, the results presented emphasize that although the spatial scales of environmental data are linked properly, model sensitivity to model characteristics such as the total number of pike in the grid and the initial pike distribution should be determined before further analyses are conducted. Moreover, Graeme (1980) found that also the timing of biological events in a CA can influence model results. Therefore we believe this should be analysed in particular before any time-dependent variation is added to the CA.

In the present study, environmental variable selection was only based on knowledge on pike ecology and behaviour from A1 publications and grey literature. However, when a model is developed to offer recommendations to local managers about a specific aquatic system, data may provide valuable additional information. Several data-driven techniques, such as classification (Gregori et al. 2010, Kampichler et al. 2010) and regression trees (D'heygere et al. 2003, 2006, Pauwels et al. 2010), artificial neural networks (Dedecker et al. 2005, Dedecker et al. 2004, Lek & Guegan 1999), support vector machines (Kampichler et al. 2010), logistic regression (Fransen et al. 2006, Kampichler et al. 2010) and fuzzy logic (Adriaenssens et al. 2004a, Adriaenssens et al. 2006, Mouton 2008, Mouton et al. 2009a, Mouton et al. 2009a, Mouton et al. 2008a, Mouton et al. 2011b, Mouton et al. 2009b) in

combination with genetic algorithms can be applied to select the main influencing environmental factors. Of course, not only these data mining techniques but also GIS datasets (Blecic et al. 2009, Li & Gar-On Yeh 2000, Yassemi et al. 2008) could easily be incorporated in a future model thanks to the discrete nature of CAs (Figure 4-2). Consequently, this approach could allow for the integration of more environmental variables (Hogeweg 1988, Toffoli 1984). A first step towards a habitat suitability model for adult pike integrating more habitat variables is presented in chapter 8 of this thesis. This model combines knowledge on pike habitat use from literature with knowledge derived from data on pike habitat use.

To further increase the model reliability, the time dependence of the HSI and a population growth module could be included. Such a dynamic HSI could depend on the season and affect pike differently based on its life stage (Inskip 1982); whereas a population growth model could integrate the system's carrying capacity and relations between different life stages. Although only one life stage was considered in the current implementation, other life stages, such as larvae and juveniles, should be integrated if a population growth model would be included. To model the population growth, a deterministic Leslie matrix model could be used, which classifies the population into life stages and simulates the abundances of each stage during a predefined number of discrete time steps (Caswell 2001). The Leslie matrix is very suitable to model a species that has only one breeding season per year, such as pike (Raat 1988), and could easily be incorporated into the current discrete CA model. Including carrying capacity could also stimulate further fine-tuning of the initial number of pike in each cell.

For the simulations presented here, the initial number of pike was chosen based on expert knowledge. However, future data collection could lead to a better quantification of the carrying capacity of the studied system and thereby increase the accuracy of the initial abundance (Craig 1996, Margenau et al. 2008). It is hereby important to note that although the presented results demonstrated the effect of the grid resolution on the model outputs, the resolution should be chosen primarily based on knowledge on the carrying capacity, the variability of the environmental variables and the scale of the addressed management issues. Constraints on the resolution could have consequences for the simulation of migration when temporally varying events are included in the model, because pike can only shift one cell per time step if a classical neighbourhood is employed. This problem is partly solved by extending the neighbourhood, however, future research is desirable to assess these consequences.

Our results indicate that the proposed CA model performs best if grid resolution is low and pike density is high. It is thus crucial to set the optimal trade-off between grid resolution and total number of pike in the grid before any further analyses are conducted or before dynamic processes are included. If model settings are carefully chosen, CAs may be practical to simulate pike migration in a river because they allow river managers to account for the effect of migration barriers on fish, in contrast to species distribution models that lack the explicit link between grid cells. However, depending on the research objectives, other modelling techniques may be more appropriate to simulate pike migration, particularly when simulations at a high resolution are required. Future research could reveal whether adaptation of the CA transition rules or other modelling techniques, such as IBM (see chapter 5), may be more suitable to model populations at a higher spatial resolution. Further, future research could focus on the integration of a growth module and the temporal dynamics of the relation between environmental factors and pike distribution.

CHAPTER 5

Exploring the opportunities of individual-based modelling (IBM) for pike migration simulation

5.1 Introduction

This study explores the usability of an individual-based model (IBM) for spatio-temporal modelling of a pike population to support river management. We propose an IBM for evolving reliable spatial-temporal distributions of pike within the same 10 km of the river Yser as described in chapter 4. This IBM takes inspiration from the one developed by Hubbard et al. (Hubbard et al. 2004) of the formation of fish schools and fish migration, extended so that (1) the IBM is adapted to mimic the dynamics of a solitary fish species, (2) it is calibrated by means of collected pike trajectory data, and (3) the model has a realistic initial condition. Although the main focus of this study is on a description of pike populations in the river Yser, it should be emphasized that the developed IBM is generic in the sense that it may be relied on for mimicking the *in situ* dynamics of other fish species in other regions after tuning its location-and species-specific model parameters.

This chapter is structured as follows. Following a brief description of the study area in Section 5.2.1, the mathematical constructs of the IBM are presented in section 5.2.2. Particular attention is paid to a quantification of the most crucial model parameters using the data of adult pike in the river Yser, gathered by radio telemetry. Moreover, the assessment of a reasonable initial distribution of the *in silico* individuals within the considered waterway and the incorporation of the migratory behaviour are given considerable attention. An evaluation of the usability of the model is presented in section 5.3, together with a validation of the proposed IBM using the collected telemetry data. Finally, the results are discussed in section 5.4.

5.2 Modelling method

5.2.1 Study area

We refer to chapter 3 for a detailed description of the study area. In the IBM the lengths of the grid cells that represent the study area represent 1 m of the length and width of the river. Consequently, the grid that represents the study area in the IBM is two-dimensional, in contrast to the one-dimensional grid in the CA based model (chapter 4).

Similarly to the CA based model, the habitat suitability in the grid cells of the IBM was determined by vegetation and bank structure data (Table 3-2). The habitat suitability was defined by a habitat suitability index (HSI; denoted η in this chapter) as in the CA based model described in chapter 4. The left and right banks were surveyed separately in the IBM and the HSI often differed between the facing river banks. Therefore, it was opted to linearly interpolate the HSI between the left and right bank in order to obtain a unique HSI at every location in the study area. Figure 5-1 visualizes the spatial distribution of the HSI within the study area together with the artificial side arms and clearly shows that the best habitats are located in the most upstream part of the study area. As in chapter 4, these side arms were assumed to be particularly suitable as spawning grounds.

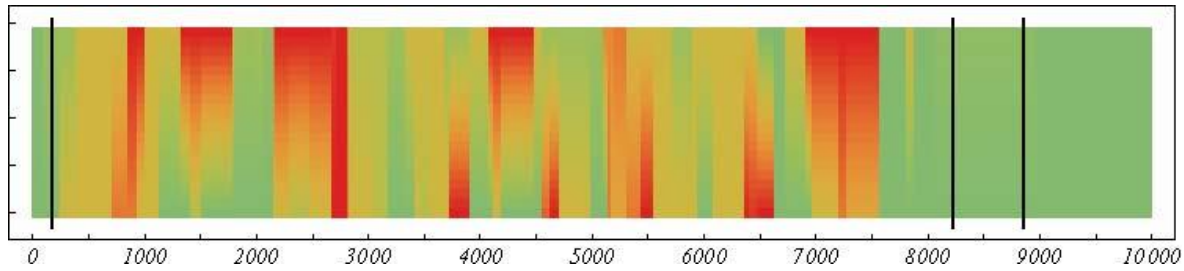


Figure 5-1: Spatial distribution of the HSI within the study area together with artificial side arms SG1, SG2 and SG3 (black vertical lines). Colours range from red (worst habitat suitability), over yellow (average habitat suitability) to green (best habitat suitability).

5.2.2 Model development

Equations of motion

Basically, the spatio-temporal dynamics of a pike individual i is governed by a vector equation that was proposed originally by Vicsek et al. (1995) to simulate the motion of interacting particles in a plane, but which has been used thereafter to describe the formation and migration of sea fish schools (Barbaro et al. 2009, Hubbard et al. 2004), as well as the movements of pedestrians (Vicsek et al. 1999). This vector equation allows to describe the position $p_i(t) = (x_i(t), y_i(t))$ of the i^{th} pike that belongs to a population of size N through time and is given by:

$$\mathbf{x}_i(t + \Delta t) = \mathbf{x}_i(t) + v_i(t) \frac{\mathbf{w}_i(t)}{\|\mathbf{w}_i\|} \Delta t, \quad (5-1)$$

where $\mathbf{x}_i(t) = [x_i(t), y_i(t)]^T$ (the location) and $v_i(t)$ is the swimming speed of the i^{th} individual. Further, $\mathbf{W}_i(t)$ is a weighted average, *i.e.*

$$\mathbf{W}_i(t) = 1 - \alpha_i(t)\mathbf{P}_i(t) + \alpha_i(t)\mathbf{Q}_i(t), \quad (5-2)$$

of two unit vectors \mathbf{P}_i and \mathbf{Q}_i that steer the direction in which pike i moves depending on the presence of other individuals in its neighbourhood and the season (\mathbf{P}_i), and the (seasonal) attraction to side arms (\mathbf{Q}_i). Using these vectors, the swimming direction θ_i of a given pike i , which is defined by the angle between the horizontal axis of an orthogonal coordinate system centered in $(x_i(t), y_i(t))$ and the vector of motion, can be obtained from

$$\begin{bmatrix} \cos \theta_i(t) \\ \sin \theta_i(t) \end{bmatrix} = \frac{\mathbf{w}_i(t)}{\|\mathbf{w}_i\|}. \quad (5-3)$$

Essentially, the weighing coefficient $\alpha_i(t)$ in Eq.(5-2) allows to alter the relative contribution of $\mathbf{P}_i(t)$ and $\mathbf{Q}_i(t)$ in the determination of $\mathbf{W}_i(t)$, which is particularly useful to mimic the dynamics of organisms that display distinct types of behaviour throughout the year. Hence, it enables a species-specific periodization of the individuals' behaviour through time.

To this day, Eqs.(5-1)-(5-3) have been used formerly to simulate the migration of school fish (Hubbard et al. 2004) such that \mathbf{P}_i follows from

$$\mathbf{P}_i(t) = \begin{bmatrix} \cos \varphi_i(t) \\ \sin \varphi_i(t) \end{bmatrix}, \quad (5-4)$$

assuming that such species align their swimming direction and velocity to each other. In Eq. (5-4) $\varphi_i(t)$ represents the average swimming direction of the fishes in the neighbourhood of an individual i , and similarly for $v_i(t)$.

Yet, as pike is a solitary predator (Maitland & Campbell 1993, Raat 1988, Webb & Skadsen 1980) that exhibits cannibalism if the competition with its congeners is too strong (Craig 1996), it is clear that the determination of \mathbf{P}_i must be altered in order to account for these specificities. Indeed, for pike it would be erroneous to assume that an individual aligns its movement with nearby individuals. Besides, modifying the determination of $v_i(t)$ and $\varphi_i(t)$ is further motivated by the fact that pike cover great distances during the spawning season, whereas they tend to be sedentary throughout the rest of the year. Evidence of such a dichotomous behaviour has been furnished by studies reporting substantial differences between the recorded swimming distances throughout one annual cycle (Harvey & Railsback 2009, Ovidio & Philippart 2003), and is further provided by studies indicating considerable fluctuations of pike's degree of activity (Koed et al. 2006).

Finally, it should be emphasized that the selection of a trustworthy initial condition from which the dynamics of an *in silico* pike population can be evolved using Eqs. (5-1)-(5-3), deserves particular attention. Not all initial spatial distributions within the river stretch at stake are equally likely as pike prefer vegetated areas (Bry 1996) and have a given home range (Donnelly et al. 1998, Malinin 1969, 1970).

In the remainder of this section we elaborate on each of the aforementioned issues and, as such, show how the model of Hubbard et al. (2004) can be extended in order to describe the *in situ* dynamics of pike in a Belgian river.

Seasonal migration behaviour

Literature on the migratory behaviour of pike suggests three periods during which adult pike show distinct migratory behaviour. Firstly, the spawning season during which pike cover big distances in order to find eligible spawning grounds (Harvey 2009, Inskip 1982). Secondly, the passive sedentary period that runs from the end of the spawning season until the start of the winter and during which pike displays a typical sit-and-wait strategy: long stationary

periods that are sporadically interchanged with sudden and short-lasting movements to catch its preys (Koed et al. 2006). Finally, the active sedentary season covering the winter months and lasting until the start of the spawning season. It is hypothesized that the latter differs from the second one because the individuals have to look for their potential preys more actively (Koed et al. 2006), which is further reinforced by the higher pike abundance that can be reached during these months following a lower cannibalistic rate (Craig 1996).

Assuming that a gradual transition occurs between the behaviour during the spawning season and during either the active or passive sedentary season fuzzy sets (Adriaenssens et al. 2004a, Adriaenssens et al. 2006, Mouton et al. 2009a, Mouton et al. 2007) were defined. The weighing function $\alpha_i(t)$ in Eq.(5-2) can be contemplated as a trapezoidal fuzzy set ($Q1, Q2, Q3, Q4$), where $Q2$ and $Q3$ denote the day numbers between which the movement of the individuals is completely driven by the attraction to the side arms, and $Q1$, and $Q4$ represent the beginning and the end of the transient, respectively. For comprehensiveness, it should be mentioned that the first of January is labelled as day number one, so that the 31st of December 2011 was assigned day number 365. Similarly to $\alpha_i(t)$, a weighing function that grasps the transition periods in which pike individuals display distinct degrees of activity was defined as a trapezoidal fuzzy set ($\phi1, \phi2, \phi3, \phi4$), where $\phi2$ and $\phi3$ denote the day numbers between which pike is passively sedentary, and $\phi1$ and $\phi4$, represent the beginning and end of the transient, respectively. Figure 5-2 visualizes an example of both transition functions in case that $\alpha_i(t) = (45, 73, 104, 134)$ and $\beta_i(t) = (104, 104, 304, 334)$.

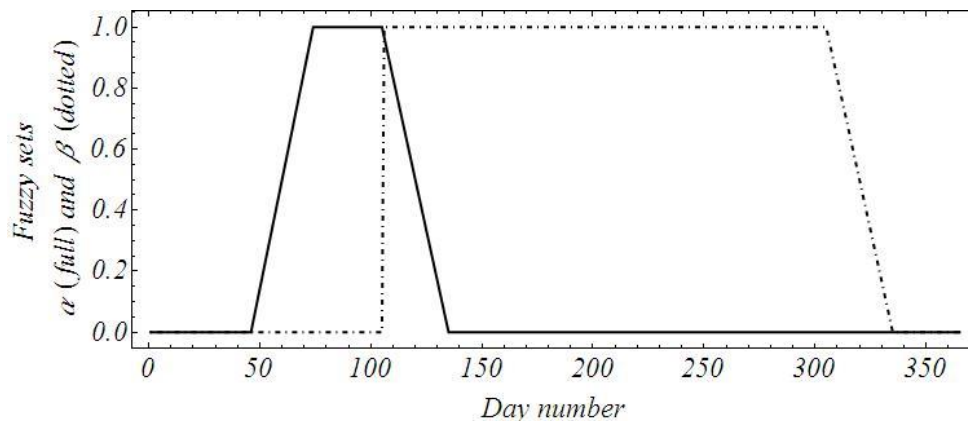


Figure 5-2: Transition functions $\alpha_i(t)$ and $\beta_i(t)$ defined as trapezoidal fuzzy sets (45, 73, 104, 134) and (104, 104, 304, 334), respectively.

To account for the discrepancies that naturally exist between individual pike, every *in silico* individual i was assigned a so-called biological clock κ_i at the beginning of an annual cycle, which indicates the day number at which the spawning season of individual i starts during the considered annual cycle, and which was drawn from a discrete uniform distribution that covers the period during which *in situ* pike individuals commence their migratory quest. In order to identify this spawning season, as well as the sedentary seasons, Figure 5-3 visualizes the average minimal daily displacement (MDD) of the tracked pike during the 12-month telemetry campaign together with the corresponding standard deviation. From this plot it was inferred that the tracked pike covered the largest distances between February 1 and May 1, so that this period was identified as the spawning season, whereas their degree of activity was minimal from May 1 until December 1 (passive sedentary season). Further, the period between December 1 and February 1 was identified as the active sedentary season. Taking into account that pike are residing about fourteen days near their spawning grounds (De Laak & van Emmerik 2006), 15-days were introduced as transition periods between every two

consecutive behavioural seasons and alpha was chosen as: $\alpha_i(t) = (\kappa_i, \kappa_i + 15, \kappa_i + 15 + 14, \kappa_i + 15 + 2 \times 14)$. Accordingly, $\beta_i(t) = (\kappa_i + 15 + 14, \kappa_i + 15 + 14, 318, 334)$, where 334 refers to the start of the active sedentary season(December1).

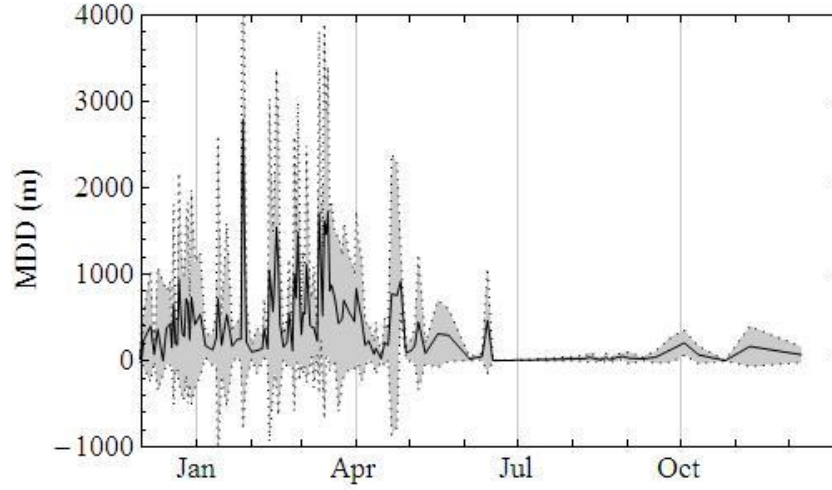


Figure 5-3: Average minimal daily displacement (MDD) of the tracked pike versus time (December 2010 –2011). The grey area corresponds to the average MDD (black line) plus/minus the standard deviation (black dotted line).

Homing

Since numerous papers report that pike exhibit territorial behaviour and have a certain home range (Donnely et al. 1998, Malinin 1969, 1970), every *in silico* individual i was assigned such a home range, which was contemplated as the radius r_i of its circular territory τ_i centred at $c_i = (x_i^T, y_i^T)$ through which pike i can swim freely. It was opted to resort to literature and a preliminary analysis of the telemetry data set in order to pin down the home ranges during the consecutive behavioural seasons because their direct assessment would have required an advanced method of analysis due to the irregularity of the sampling intervals (Katajisto & Moilanen 2006), which was considered beyond the scope of this chapter that is of a more generic nature. During the passive sedentary season r_i was chosen 50 meters, being the lower bound of the interval of home ranges reported by Donnely et al. (Donnely et al. 1998) and in agreement with the findings of Goethals et al. (Goethals et al. 2006) who report that the majority of pike in the Flemish rivers are retrieved at less than hundred meters from the site where they are first captured. On the other hand, a preliminary analysis of the telemetry data set allowed to infer a considerably higher home range during the active sedentary season, namely $r_i = 2000$ m. During the spawning season pike are not bound to their territory ($\alpha_i = 1$), such that no r_i had to be chosen. Further, disregarding intra species variability, the home range was assumed the same for all individuals within the population, such that we may write $r = r_i$ for all i .

Swimming direction

Taking into consideration that pike exhibit territorial behaviour outside the spawning season, $\phi_i(t)$ in Eq.(5-4) could not be computed by averaging the speed of nearby individuals, which is plausible for school fish, but rather using

$$\phi_i(t) = \beta_i(t)\phi_i^l(t) + (1 - \beta_i(t))\phi_i^a(t), \quad (5-5)$$

which is a β -weighted sum of the behaviour during the passive sedentary season, i.e.:

$$\varphi_i^2(t) = \begin{cases} E(p_i(t)), & \text{if } d(p_i(t), c_i) > 50 \text{ or } (\exists j) \left(d(p_i(t), p_j(t)) \leq 10 \right) \\ \theta_i(t) + \xi_i, & \text{else} \end{cases} \quad (5-6)$$

where $d(p_i(t), p_j(t))$ denotes the Euclidean distance between $p_i(t)$ and $p_j(t)$ and similarly for $d(p_i(t), c_i)$, $E(x_i(t)) = \arctan(x_i(t) - x_i^T, y_i(t) - y_i^T) + \pi$ expresses that pike i swims in the direction of its territory centre if it encounters a congener or crosses the outskirts of its territory, and ξ_i denotes a random perturbation of $\theta_i(t)$ for which it holds that $\xi_i \sim U\left(-\frac{\pi}{4}, \frac{\pi}{4}\right)$, and the one observed during the active sedentary season, i.e.:

$$\varphi_i^3(t) = \begin{cases} E(p_i(t)), & \text{if } d(p_i(t), c_i) > 2000 \\ \theta_i(t) + \xi_i, & \text{else} \end{cases} \quad (5-7)$$

Informally, Eq. (5-6) expresses that an *in silico* individual will not change its swimming direction deliberately during the passive sedentary season unless it encounters a congener at less than 10 m ($d(p_i(t), p_j(t)) \leq 10$) or it crosses the boundary of its territory ($d(p_i(t), c_i) > 50$). Similarly, Eq. (5-7) governs the behaviour of the *in silico* individuals during the active sedentary season in such a way that they will only change their swimming direction intentionally if they cross the boundaries of their territories ($d(p_i(t), c_i) > 2000$). Beside the intended and directed changes, Eqs.(5-6) and (5-7) capture the stochasticity of the swimming process by perturbing the swimming direction in absence of an external stimulus. Since $\alpha_i = 1$ during the spawning season, the swimming direction will then be determined completely by the attraction towards the side arms that is embodied in $Q_i(t)$. The attraction to a side arm SG was described by means of a potential function $\Phi(x, y)$ that quantified this attraction at each location in the study area, such that $Q_i(t)$ in Eq. (5-2) was obtained from a potential gradient $\nabla\Phi(x, y)$ i.e.:

$$Q_i(t) = \frac{\nabla\Phi(x_i(t), y_i(t))}{\|\nabla\Phi(x_i(t), y_i(t))\|} \quad (5-8)$$

Naturally, if there are multiple side arms SGs in the study area, *in silico* individuals will be partially attracted to each of them, which can be expressed mathematically by aggregating individual potential functions $\Phi_s(x_i(t), y_i(t))$, i.e. one for every side arm SGs. As such, $\Phi(x_i(t), y_i(t))$ in Eq. (5-8) should be replaced by $\Theta_s^s[\Phi_s(x_i(t), y_i(t))]$, where Θ_s^s represents an aggregation function.

In order to express the attraction of pike towards a side arm SGs in the river Yser during the spawning season, a potential function $\Phi_s(x, y)$ as proposed originally by Magnusson et al. (2004) was defined as:

$$\Phi_s(x, y) = -\frac{m}{2\pi} \ln d((x, y), (x_s, y_s)), \quad (5-9)$$

in which (x_s, y_s) denotes the centre of SGs, and m is the total attraction to the side arms that was assumed to be one. Taking into account the presence of multiple side arms suitable for spawning in the concerned river stretch (Figure 3-7), *in situ* individuals will be partially

attracted to each of them. Yet, it is likely that an individual will prefer the side arm that is located the closest since this requires the smallest energy loss due to migratory movements, such that the overall potential function was written as $\max_k \Phi_k$. The potential functions Φ_1, Φ_2 and Φ_3 corresponding with the side arms SG1, SG2 and SG3, respectively, as well as the overall potential function $\max_k \Phi_k$ along the river stretch at stake are sketched in (Figure 5-4).

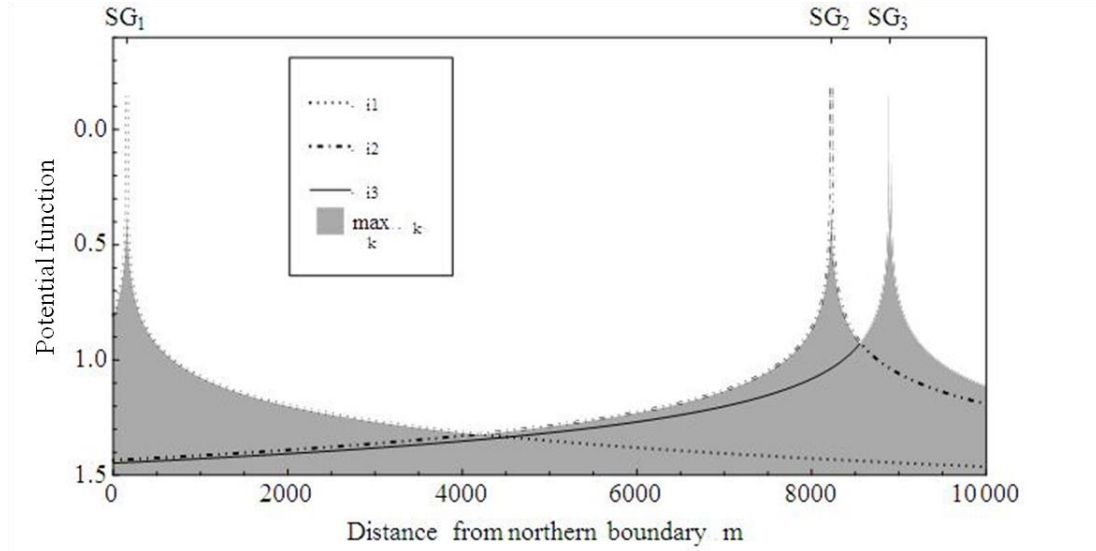


Figure 5-4: Potential functions Φ_1, Φ_2 and Φ_3 corresponding with the side arms: SG1, SG2 and SG, together with the overall potential function $\max_k \Phi_k$ (shaded area).

Swimming speed

Since the preliminary analysis of the telemetry data gathered during the spawning season revealed that the MDD obeyed a Weibull distribution, the swimming speed, expressed in meter per day, of every individual i and at every consecutive time step was drawn from a Weibull distribution $W(\lambda, k)$, where λ represents the shape parameter and k is the scale parameter, determined using the maximum likelihood method (Harris & Stocker 1998). We assessed that $\lambda = 0.60$ and $k = 406.03$, such that $\tilde{v}_i^1(t) \sim W_1(0.60, 406.03)$, where \tilde{v}_i^1 denotes the swimming speed of an individual i at a given t during the spawning season. Similarly, the individual swimming speeds during the passive and active sedentary season, denoted as \tilde{v}_i^2 and \tilde{v}_i^3 , respectively, were drawn from Weibull distributions that were parameterized using data on the MDD that were collected during these behavioural seasons in the framework of the aforementioned telemetry study. More precisely, it was found that $\tilde{v}_i^2(t) \sim W_2(0.45, 48.82)$ and $\tilde{v}_i^3(t) \sim W_3(0.60, 262.23)$. In order to account for the vague transition between the subsequent behavioural seasons, which is formalized by fuzzy sets $\alpha_i(t)$ and $\beta_i(t)$, the effective swimming speed of an individual i was obtained from:

$$v_i(t) = \alpha_i(t)\tilde{v}_i^1 + (1 - \alpha_i(t))[\beta_i(t)\tilde{v}_i^2 + (1 - \beta_i(t))\tilde{v}_i^3(t)] \quad (5-10)$$

This equation stipulates that the effective swimming speed of an *in silico* individual was determined as a weighted sum of its swimming speed during the spawning season $\tilde{v}_i^1(t)$ and the one in the two other seasons, where the latter was computed as a weighted sum of the swimming speeds during the active and passive sedentary seasons. This is illustrated in Figure

5-5 that shows the effective swimming speed of an individual during one annual cycle if $\tilde{v}_i^j(t)$ in Eq. (5-10) is replaced by the average recorded MDD of the corresponding behavioural season, being 613, 122 and 404 m day⁻¹, respectively.

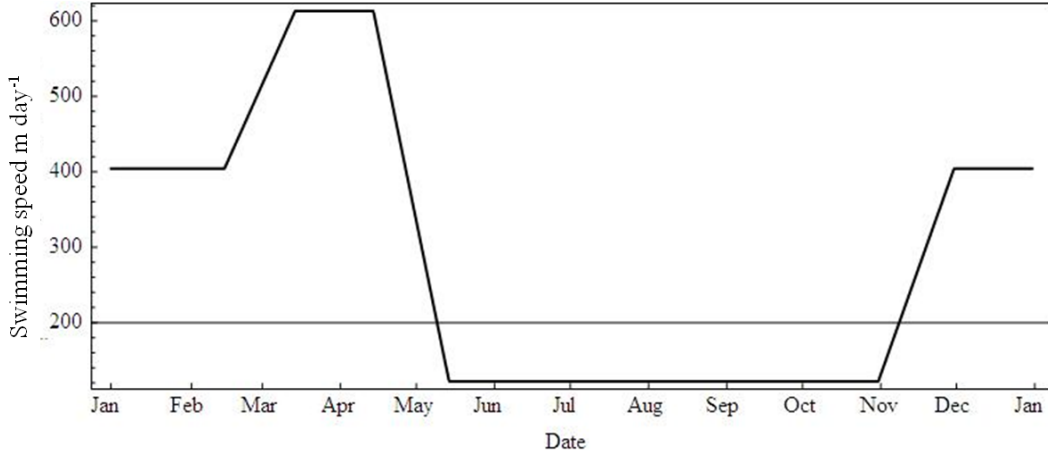


Figure 5-5: Effective swimming speed of a pike individual during one annual cycle as given by Eq. (5-10) in which $\tilde{v}_i^j(t)$ is replaced by the average MDD of the corresponding behavioural season.

5.2.3 Initial and boundary conditions

As mentioned before, every pike i has to be assigned a territory τ_i with centre \mathbf{c}_i that is located within the concerned river stretch because pike are solitary, homing, and sporadically cannibalistic beings (Craig 1996, Donnelly et al. 1998, Malinin 1969, 1970). Once these territories have been assigned, it can be assumed that $\mathbf{x}_i(0) = \mathbf{c}_i$ to initiate model simulations. As such, we ought to allocate the territories realistically across the study area in order to set up a lifelike initial pike distribution from which the spatio-temporal dynamics can be evolved using the proposed IBM.

Essentially, the allocation of territories may be seen as an optimization problem since it is natural to assume that a pike individual will try to minimize the overlap between its own territory and the one of individuals in its vicinity because it is a solitary species (Craig 1996), while at the same time it will try to maximize the area of its τ_i that is located in parts of the river that are well-suited for sustaining pike. The latter can be quantified by means of a habitat suitability index, denoted η . By relying on the methodology proposed by González (2003) for finding the optimal distribution of wireless sensors, the first condition can be expressed mathematically as the minimization of:

$$O_1 = \sum_i \sum_{j \neq i} e^{-d(c_i, c_j)^2 r^{-2}}, \quad (5-11)$$

where $d(c_i, c_j)$ denotes the Euclidean distance between c_i and c_j . The contribution of each of the exponential terms in the right-hand side (RHS) of Eq. (5-10) can be at most one if and only if $c_i = c_j$, and approaches zero if $d(c_i, c_j) \geq 2r$. This is illustrated more clearly in Figure 6, which shows O_1 as a function of $d(c_i, c_j) r^{-1}$ in the case the fish population consists of only two individuals i and j .

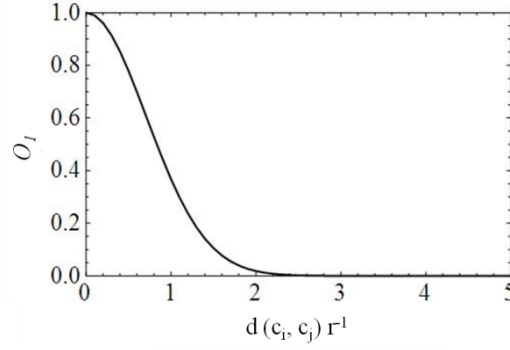


Figure 5-6: Penalty function O_1 (Eq. (5-10)) versus $d(c_i, c_j) r^{-1}$.

The second constraint on the allocation of the territories, namely the maximization of their habitat quality or, equivalently, the minimization of the territories' area that is located in regions with low HSI, could simply be formulated as the minimization of

$$O_2 = \sum_i 1 - \eta(\tau_i), \quad (5-12)$$

where $\eta(\tau_i)$ represents the HSI at c_i .

Clearly, O_1 and O_2 could be merged in one integrated objective function that can then be used for allocating the territories among the fishes within the population. Yet, attention should be paid to the relative weight that is assigned to each of the constraints. More specifically, this traces back to assessing how much overlap $2fr$ ($f \in [0,1]$) an individual j will tolerate with another τ_i if this overlap maximizes $\eta(\tau_j)$. This can be assessed by taking into account that the term in the RHS of Eq. (5-11) increases by $\exp(-(2-2f)^2)$ as the overlap between τ_i and τ_j increases from zero to $2fr$, whereas the RHS of Eq. (5-12) decreases by $\bar{\eta} - \underline{\eta}$ (where $\bar{\eta}$ and $\underline{\eta}$ represent the maximum and minimum HSI in the study area, respectively) if the territory of j is located in a region that maximizes its HSI but also entails an overlap $2fr$. Hence, normalization of the RHS of Eq. (5-12) by $\frac{\bar{\eta} - \underline{\eta}}{\exp(-(2-2f)^2)}$ entails that an individual will tolerate an overlap of $2fr$ as long as this leads to $\eta(\tau_j) = \bar{\eta}$, such that the integrated objective function can be written as:

$$\tilde{O} = \sum_i \left(\sum_{j \neq i} e^{-d(c_i, c_j)^2 r^{-2}} + (1 - \eta(\tau_i)) \frac{e^{-(2-2f)^2}}{\bar{\eta} - \underline{\eta}} \right). \quad (5-13)$$

To clarify the above reasoning, consider a pike j of which the territory should be located in a river stretch where $\bar{\eta} = 0.8$ and $\underline{\eta} = 0.3$, and which is already occupied by another pike i .

Hence, it is clear that the second term in Eq. (5-13) decreases by $\bar{\eta} - \underline{\eta} \frac{e^{-(2-2f)^2}}{\bar{\eta} - \underline{\eta}} = e^{-(2-2f)^2}$ if τ_j can be assigned to a part of the river stretch where the HSI is maximal as opposed to an allocation to a region where $\eta(\tau_j) = \underline{\eta}$. Accordingly, as long as the additional contribution of the first term in the RHS of Eq. (5-13) due to a possible overlap between τ_i and τ_j that is required to maximize $\eta(\tau_j)$, remains smaller than $e^{-(2-2f)^2}$, j will accept this overlap. Of course, such a trade-off only arises if all stretches within the river where the HSI is maximal are already occupied prior to the introduction of j .

In the remainder of this paper, it is assumed that a pike opts for a maximization of its $\eta(\tau_i)$ as long as the overlap this might bring forth is smaller than one half of its territory's radius

($f = \frac{1}{4}$). Further, it is opted to exclude the artificial side arms as possible territories, such that the factor $\frac{e^{-(2-2f)^2}}{\bar{\eta}-\eta}$ in the RHS of Eq. (5-13) equals approximately $\frac{1}{5}$.

Finally, it is clear that boundary conditions should be imposed to avoid individuals from leaving the river stretch if their position at $t + \Delta t$ given by Eq. (5-1) would be located outside the study area. Within the framework of this paper, reflecting boundary conditions are used to mimic the movement of pike that are approaching the river banks as faithfully as possible. This kind of boundary conditions dictates that such individuals are reflected at the boundaries of the study area, which either represent the river bank or the in- or outlet of the concerned river stretch, if $\mathbf{x}(t + \Delta t)$ is located outside the study area. More precisely, the line connecting $p_i(t)$ and $p_i(t + \Delta t)$ that intersects with the study area's boundary is reflected on this boundary at the point of intersection in such a way that the incoming angle equals the outgoing one. The swimming direction of reflected individuals then becomes $\pi - \theta_i(t)$ or $2\pi - \theta_i(t)$ if the reflection occurs at a vertical or horizontal boundary, respectively.

5.3 In silico experiments

5.3.1 Initial condition and side arms

It was supposed that $N = 50$ as this agrees with the lower bound of the carrying capacity range that is mentioned in literature (Craig 1996). Further, Eq. (5-13) was minimized using simulated annealing (Kirkpatrick et al. 1983), which is a well-established algorithm for numerically optimizing functions. Seen this optimization procedure can be time-consuming if the population consists of a relatively large number of individuals, we opted to minimize Eq. (5-13) by successively adding one individual to the population, allocating its territory such that Eq. (5-13) is minimized under the condition that the position of already allocated territories remains unchanged and repeating this procedure until each individual in the populations was assigned a territory. It was verified that the allocation of the territories by relying on this approach did not significantly differ from the one obtained by assigning them concurrently. Comparing Figure 5-7, which shows the location of the territories that are assigned to the individuals within the population at stake, and the spatial distribution of the HSI clearly unveils that the majority of them are situated in those stretches of the river that are characterized by a high HSI. This is further confirmed by Figure 5-8, which depicts the relative frequency distribution of both the number of territories and the surface area within the concerned river stretch versus the HSI, as the distribution of the former is patently shifted towards the higher end of the HSI range compared to the one of the surface area.

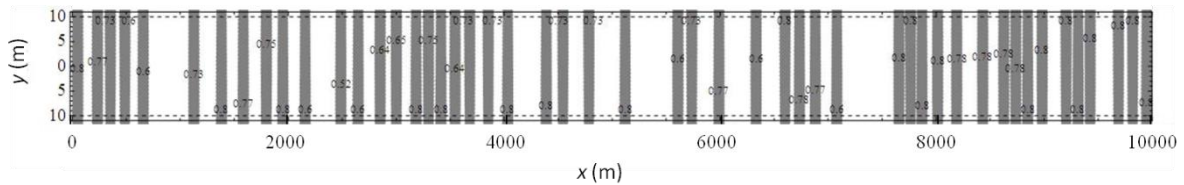


Figure 5-7: Location of the territories of the 50 pike within the considered population, which is optimized numerically according to Eq. (5-13).

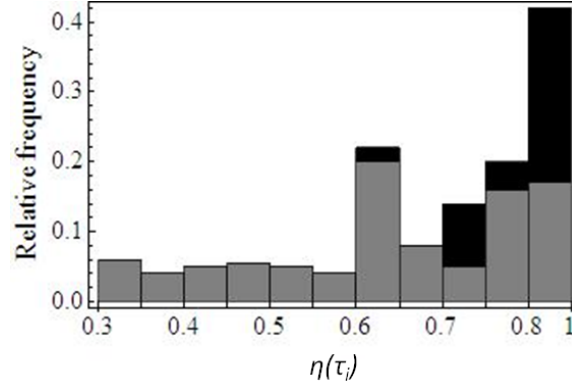


Figure 5-8: Relative frequency distribution of the number of territories (black) and the surface area (grey) within the concerned river stretch versus the HSI.

5.3.2 An annual cycle

Within the framework of the *in silico* experiments, we chose $\Delta t = 3600$ s. Figure 5-9 shows snapshots of the simulated spatial pike distribution within the study area at the beginning of six different days during an annual cycle. The dates at which snapshots are shown, were selected such that the movement patterns during both the sedentary and spawning season can be inferred from Figure 5-9. From the first snapshot, which is taken prior to the start of the spawning season, it is obvious that all members of the population are residing within their territory, whereas, at March, 2, some pike (colored grey) are already migrating towards the side arms for spawning nonetheless the majority of the individuals is still found within their territory. During the next weeks, the number of pike that starts its journey towards the side arms gradually increases and by the second of May most of them can be retrieved near one of the artificial side arms. Finally, as the migration season ends at the latest by the end of May, all individuals return to their territories where they can be retrieved during the summer months and the remaining part of the year.

Of course, the spatio-temporal distribution depicted in Figure 5-9 is just one possible realization brought forth by simulation of the developed IBM from the given initial condition (cfr. Figure 5-7) owing to the stochasticity that is involved through the assessment of the swimming direction and speed by means of Eqs. (5-6) and (5-7), and Eq. (5-10), respectively. Hence, in order to acquire a reliable understanding of the individuals' spatio-temporal dynamics it is imperative to generate a predefined number of realizations by repeatedly simulating the spatio-temporal species distributions and draw conclusions on time series of distributions of macroscopic characteristics that are computed thereafter over both the realizations and the individuals within the population at stake. Throughout the remainder of this paper, 100 realizations of the established IBM are underlying the discussion and conclusions.

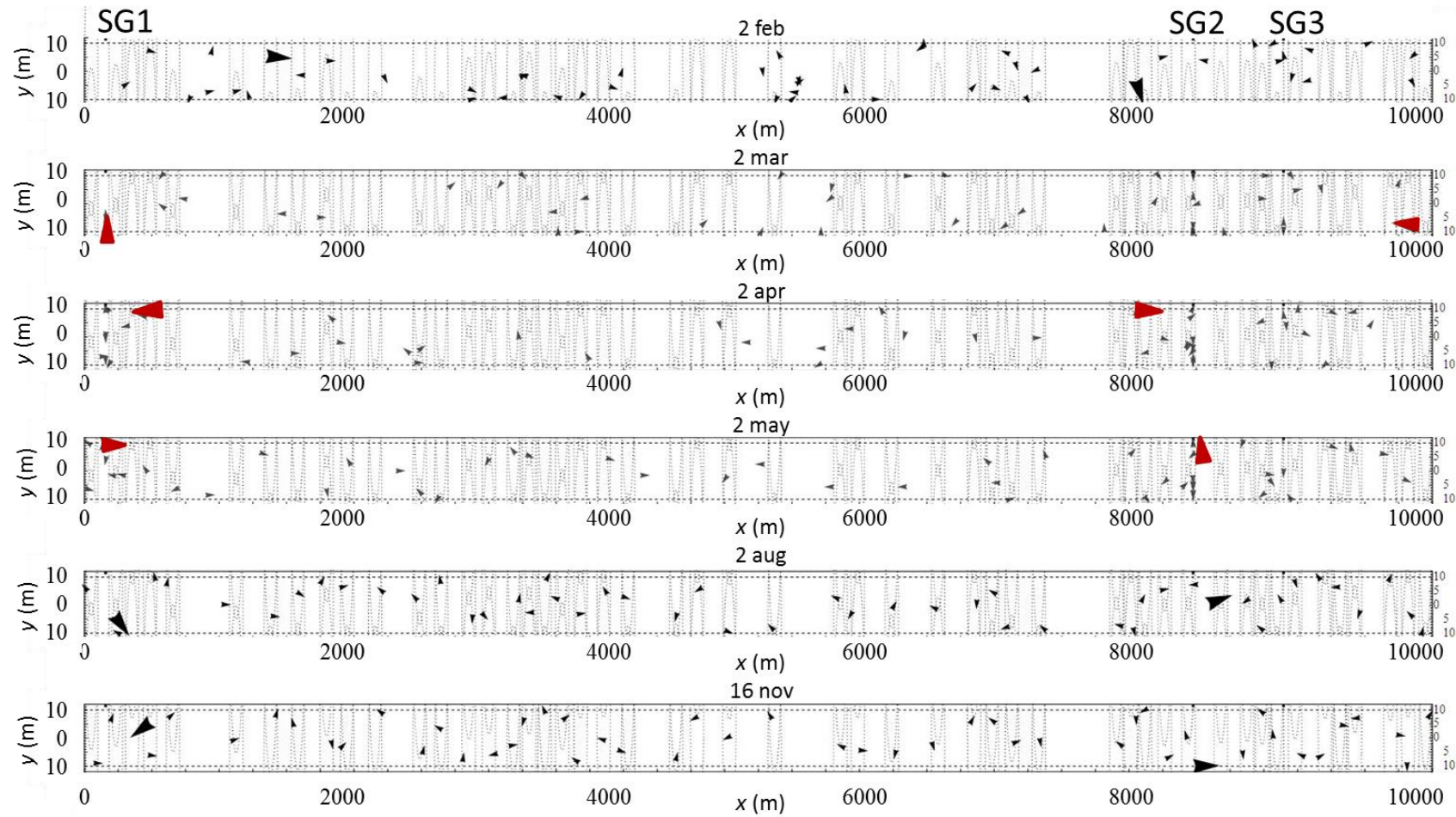


Figure 5-9: Simulated spatial distribution of the individuals (arrowheads) within the study area at the beginning of six different days during an annual cycle together with the territories (dotted lines) determined by minimization of Eq. (5-13). The individuals, of which two are shown by large arrowheads for tracking purposes, are represented by black arrowheads if $\alpha_i(t) = 0$ and red arrowheads if $\alpha_i(t) > 0$. The side arms, assumed to be used as spawning ground, are indicated as SG_k .

Figure 5-10 visualizes the average distance between c_i and $p_i(t)$ during an annual cycle together with the average speed of the individuals within the population at stake, which are calculated over both the 100 realizations of the IBM and the individuals. The shaded area always illustrates the envelop in which 95 % of the realizations is retrieved. From the former it can be inferred that the average distance remains approximately 1000 m until the beginning February, which can be understood by recalling that pike move almost randomly within their territory with radius 2000 m during the active sedentary season. Yet, as soon as the migration seasons commences the average distance increases to about 1100 m. Furthermore, during the latter season the distance between c_i and p_i is highly variable between the populations' individuals, which can be attributed to the fact that some individuals are already migrating, whereas others are still residing in their territories (Figure 5-11). Besides, the territory of some *in silico* individuals was centred in the direct vicinity of an artificial side arm, so that these organisms had no urge to cover a large distance in order to reach a side arm suitable for spawning, as opposed to individuals whose territory was located at a greater distance from such an artificial side arm. Clearly, this variability almost vanishes once the pike return to their territories since they then enter the passive sedentary season during which they are highly sedentary. Similar observations can be made with regard to the swimming speed that is depicted in Figure 5-10 and which relate to the different degrees of activity that pike tend to show throughout one annual cycle (cfr. Eq. (5-10)).

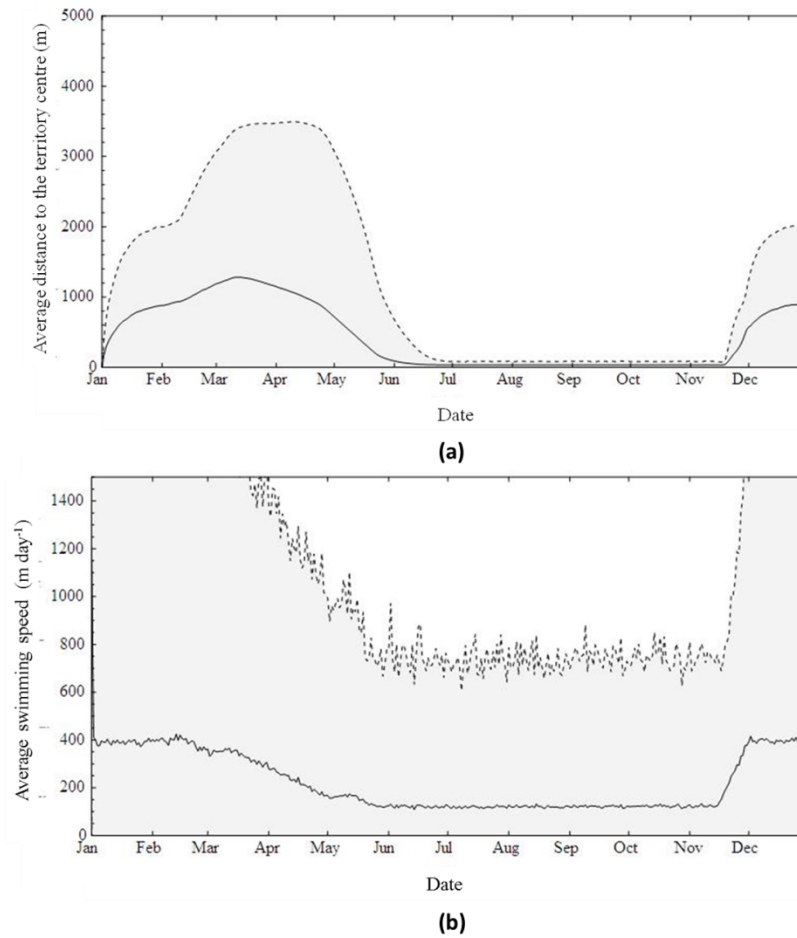


Figure 5-10: Average distance between c_i and $p_i(t)$ (a) and average swimming speed (b), which are obtained by averaging over both the realizations of the IBM and the individuals. The shaded area illustrates the envelop in which 95 % of the realizations is retrieved.

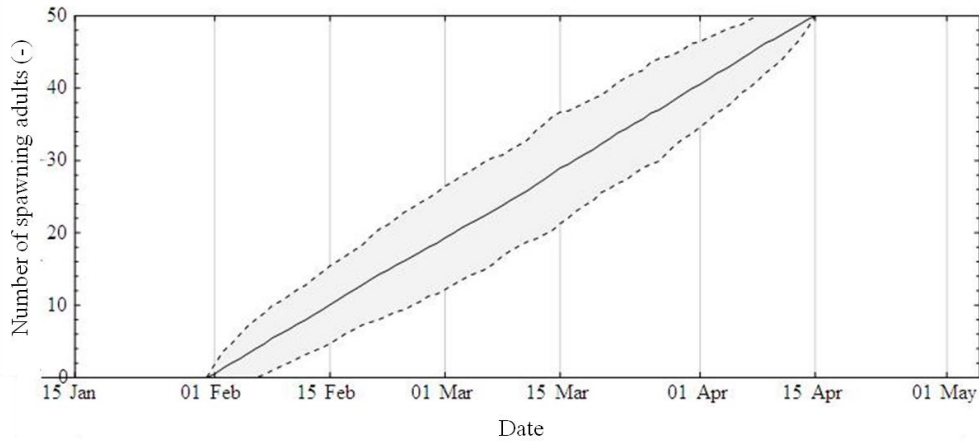


Figure 5-11: Average cumulative number of pike that started its migratory movement towards one of the side arms, which is obtained by averaging over both the realizations and the individuals. The shaded area illustrates the envelop in which 95 % of the realizations is retrieved.

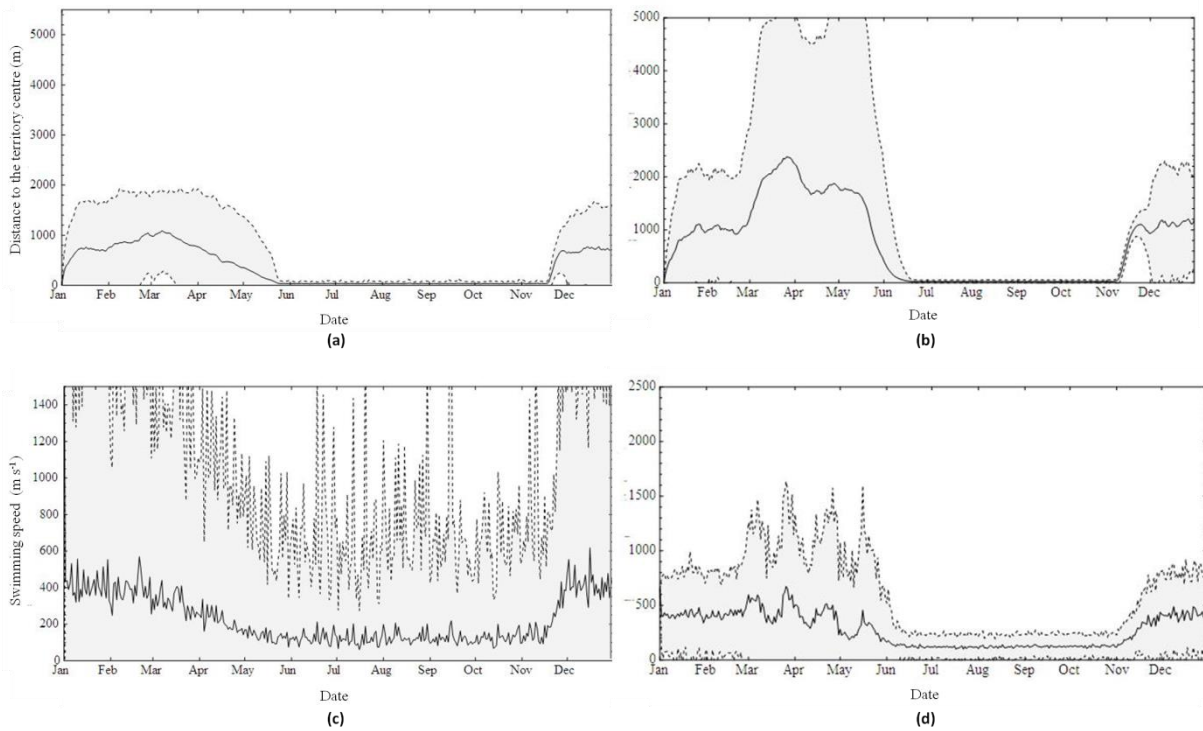


Figure 5-12: Distance between c_i and $p_i(t)$ (a and b) and Swimming speed (c and d) for two individuals of the population at stake. The values are obtained by averaging over the IBM realizations. The shaded area illustrates the envelop in which 95 % of the realizations is retrieved.

In order to gain insight into the variability of a given individual's characteristics across the 100 realizations, which gets blurred by representing averages over both the realizations and individuals, Figure 5-12 shows the average distance between two given individuals and their territory during one annual cycle, as well as their average swimming speed, which are both obtained by averaging only over the realizations of the IBM. Although the average distance between c_i and $p_i(t)$ during the spawning season is considerably small for one of the tracked

individuals (attributed to the fact that its territory is located relatively close to a side arm) this figure clearly shows that the overall behaviour of the two tracked individuals coincides with the tendencies that have been observed with regard to the entire population (Figure 5-10). This is particularly true for the swimming speed.

5.3.3 Validation of the simulation results

Since a profound validation of the developed IBM would require a much vaster data set than the one collected in the framework of the tracking campaign in the river Yser, Belgium, between November 2010 and December 2011, and the principal scope of this chapter is the formalization of a modelling framework for describing the spatio-temporal dynamics, we will show the similarity between the outcome of the *in silico* experiments and the real-world observations on the movement of pike in the river Yser. As such, we grant the usability of the proposed IBM in the framework of similar settings. Taking into consideration the stochastic nature of the IBM, which is caused by drawing the swimming speed of individual fish at every time step from the parametrized Weibull distributions W_1 , W_2 and W_3 , and by perturbing the swimming direction, it should be clear that there can never be a one-to-one correspondence between the real-world trajectory of a given pike individual and its *in silico* counterpart. Indeed, in such a setting the trustworthiness of the IBM should not be evaluated by assessing the discrepancies between a given observed trajectory and an *in silico* one, but rather by showing that the formers constitutes a possible and plausible validation of an *in silico* experiment. Since a series of *in silico* experiments yields a distribution of positions for every *in silico* individual, one can show the validity of the proposed IBM if one is able to show that a given real-world trajectory could have been drawn from one such a distribution. More specifically, taking into account the homing behaviour of pike, the observed trajectory of a pike individual that has its territory at \mathbf{c}_i should constitute a possible realization of the distribution that reflects the positions of an *in silico* individual that has its territory centred near \mathbf{c}_i throughout an annual cycle.

Figure 5-13 depicts the average position of an *in silico* individual of which the territory is centred near the one of the real-world individual for which the registered positions during 2011 are depicted as black dots together with the corresponding confidence interval. Two conclusions can be drawn immediately from this figure. Firstly, it is clear that the observed positions throughout the annual cycle are not located on the curve that connects the average position of the corresponding *in silico* individual, but nonetheless they are often located relatively close to that line or to the dashed lines that indicate the border of the 95 % confidence interval. Secondly, it is obvious that the overall patterns that can be inferred from the positional data of the real-world individual, such as the relatively steady position during the passive sedentary season and the significantly more pronounced positional fluctuations during the active sedentary and spawning seasons, are also inherent to the dynamics of the *in silico* individual. This comes forward by the much wider/broader confidence interval during the former season, as opposed to their width in the latter ones. The latter similarity indicates that the proposed IBM captures the differences in pike dynamics between the distinct behavioural seasons. Moreover, in agreement with the tracking data, the simulation results indicate that the concerned individual does not undertake a migratory quest, which can be attributed to the presence of a side arm near the centre of its territory. The agreement between the *in silico* and *in situ* dynamics was further confirmed by means of the washer method (Venturini 2011), which indicated for the real-world individual at stake that only 19 % of the observations did constitute outliers of the *in silico* time series distributions. Similar findings were made with regard to the agreement between the simulated and observed dynamics for

other pike individuals that spent the largest part of the annual cycle in the modeled river stretch.

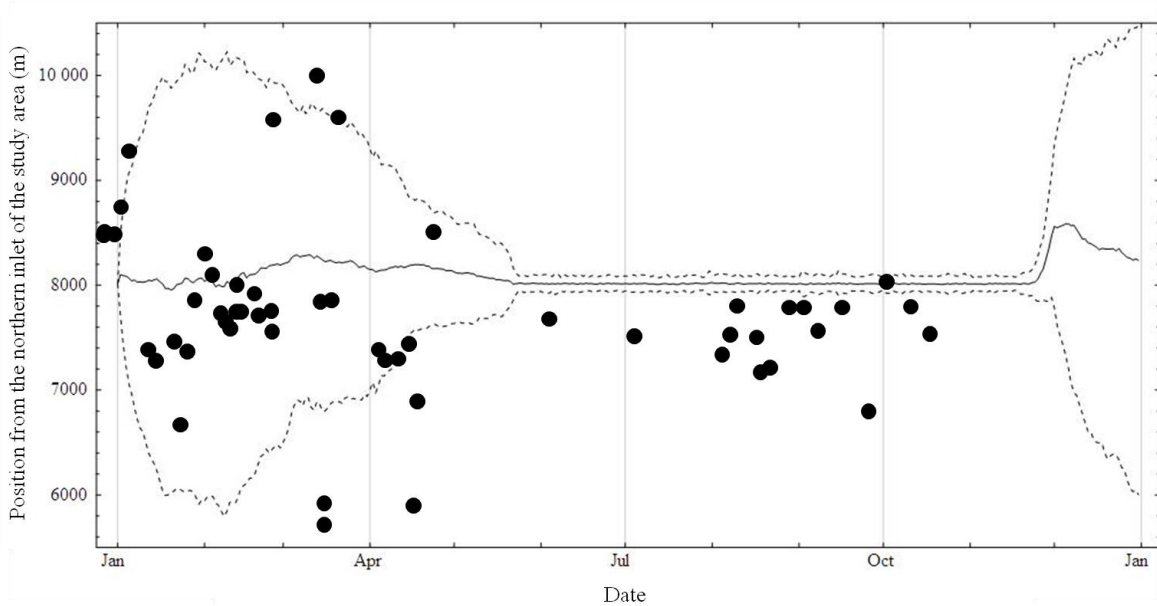


Figure 5-13: Average position of an *in silico* individual (black line and corresponding confidence interval (dashed lines)) of which the territory is centred near the one of a real-world individual for which the positions were collected during the telemetry campaign of 2011 (black dots).

Aside from the fact that the IBM should yield an ensemble of trajectories that encloses the real-world one, it is important that it somehow grasps the *in situ* interaction between pike individuals in order to grant its validity even further. The comparability between the *in situ* and *in silico* interaction is demonstrated in Figure 5-14 which shows the normalised pairwise distance, *i.e.* the pairwise distance normalized by the length of the river stretch, between *in situ* and *in silico* pike individuals throughout the considered annual cycle. It is immediately clear from this figure that the absolute values of this quantity are different from one another, but this can be understood by drawing attention on the unequal number of *in silico* and *in situ* individuals, on the one hand, and the discrepancy between the length of the modelled river stretch and the one through which the tagged pike could freely move, on the other hand. Besides, in the *in silico* experiments one keeps track of the entire pike population in the modelled river stretch, whereas only a small subsample of the *in situ* population was followed during the tracking study. Aside from the discrepancies between the absolute values of this quantity, Figure 5-14 indicates that the increased repulsion between *in situ* individuals during the spawning season is captured by the developed IBM because the pairwise distance between *in silico* individuals is clearly augmented during that season, just as in case of the tracked subpopulation.

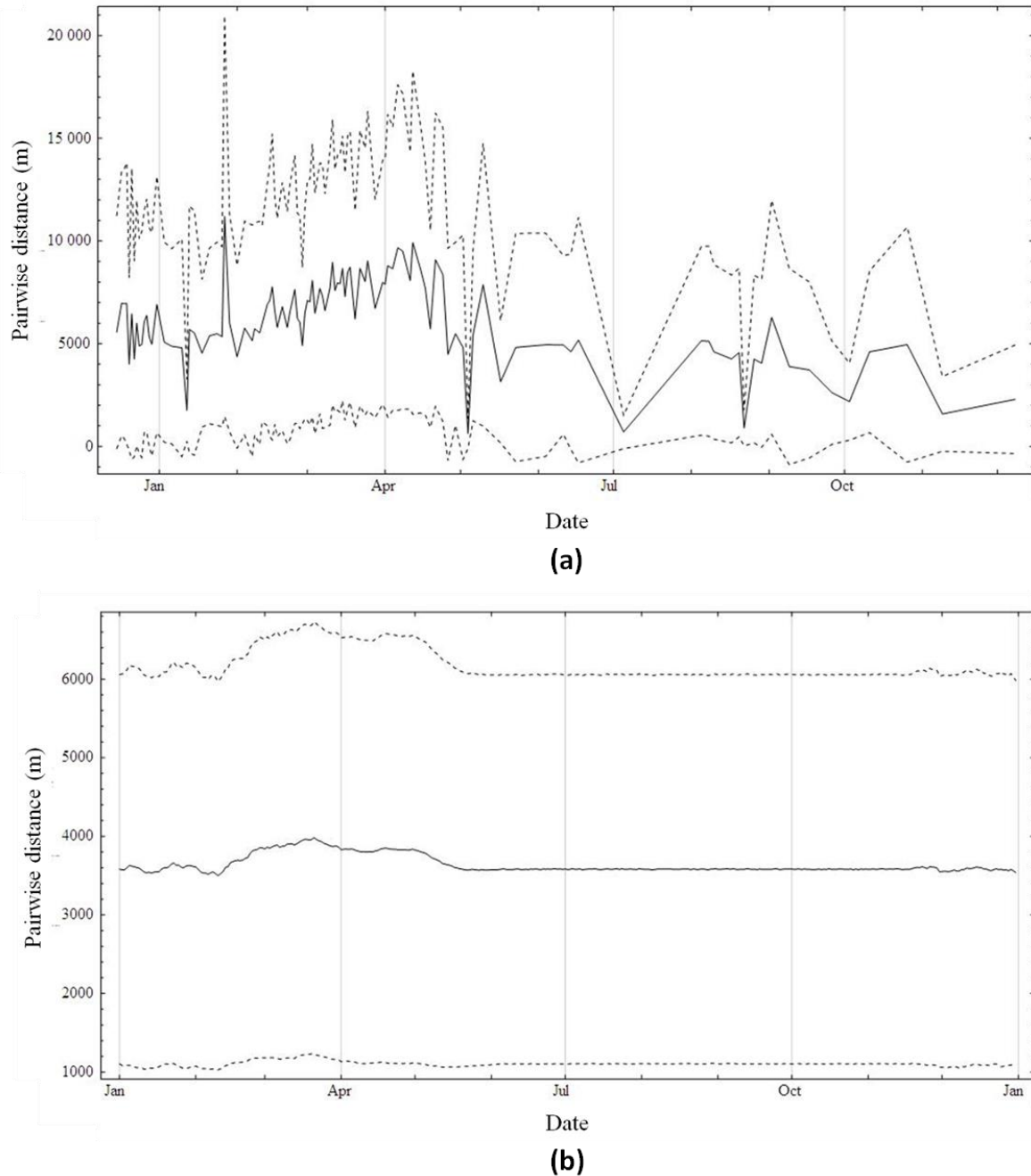


Figure 5-14: Pairwise distance between in situ (a) and in silico (b) individuals during an annual cycle in 2011.

5.4 Discussion

Even though the developed IBM is presented for understanding the spatio-temporal dynamics of pike in the river Yser, Belgium, it is generic in the sense that it can be tuned easily if another fish species is at stake by tuning its parameters using species-specific tracking data. Especially the transition functions $\alpha_i(t)$ and $\beta_i(t)$ as well as the specificities of the species' territories, *i.e.* the variability of the home range throughout one annual cycle, deserves particular attention if one aims at using this model within the framework of another species. The same applies on using the model for pike in another river system, in which case the initial HSI map and potentially the dimensions of the territories differ. Further, the swimming speed

should be drawn from distributions that are based upon data originating from tracking or recapturing experiments in the concerned study area and it should not be forgotten that a HSI map of this area, which takes into account the environmental characteristics that are known to affect the particular species, has to be assembled since this is crucial for setting up a trustworthy initial spatial distribution of the individuals. In this paper, the home range during the passive sedentary season was inspired on values that were found in literature (Donnelly et al. 1998), whereas the one during the active sedentary season was based upon a preliminary analysis of the tracking data that were collected in the study area. This was motivated by the fact that a direct assessment of these home ranges would require advanced methods of analysis, which was considered beyond the scope of this chapter that is of a more generic nature. Yet, within the framework of species- and location-specific studies, these values should be determined by means of dedicated methods of analysis using ample tracking data (Katajisto & Moilanen 2006). Analogously, these data should be exploited to obtain the experimental distribution that is underlying the swimming speed, as well as to delimit the different behavioural seasons.

In spite of the common knowledge that most species tend to occupy those habitats within the ecosystem that are most suited to sustain them, which is particularly true for solitary fish species such as pike, IBMs are often evolved from a random initial distribution. As such, this compromises the trustworthiness of the IBM simulations from the very beginning of the concerned simulation period, which can however be overcome by determining an *in silico* initial condition that reflects a realistic distribution of the *in situ* individuals' positions. Generally, such approach leads to an optimization problem, such as the one defined by Eq. (5-13) for establishing a trustworthy initial pike distribution. The procedure followed in this chapter for minimizing Eq. (5-13) and which comprises the stepwise solution of this optimization problem by assigning the territories consecutively as individuals are added to the population, requires significantly less computing time than solving it by simultaneously optimizing the allocation of the territories of all individuals within the concerned population. In addition, it is certainly not unlikely that such a stepwise optimization, and hence territory allocation, resembles the real-world situation more naturally since juvenile pike that are trying to establish their new territories will thereby be hindered by pike that already settled theirs.

Since it is presumed that pike is a solitary species that sticks to the same territory throughout its life, a pike's territory is not reallocated once it has been pinned down by minimizing Eq. (5-13). Though this presumption is based upon findings in literature (Malinin 1969, 1970), a recent study in south Belgium revealed that only three out of six tracked fish returned at the end of the spawning season to the same territory as the one they occupied before they started their migratory quest (Ovidio & Philippart 2003), which is in line with the observations of Diana (1977). If future studies would confirm this finding, a (partial) reallocation of the territories at the end of the spawning season should be incorporated into the model. Similarly, if tracking data would reveal a clear relationship between the position of an individual within its territory and the HSI at that particular location, the IBM can be extended easily to take such findings into account since the current model structure allows them to move freely within their territory. Of course, this would require accurate knowledge of the environmental conditions that steer the HSI at a high spatial resolution, which might be difficult to acquire. Finally, it is beyond question that the current model structure merely takes into account the spatio-temporal movements of pike, whereas an integrated population model would require a coupling between the migration module presented in this thesis, on the one hand, and a growth model for pike, for which one could rely on a spatial version of a Leslie-matrix model that has been proposed only recently for describing temporal density fluctuations (Arlinghaus et al. 2009, 2010), on the other hand.

Aside from the quantitative agreement between the *in silico* and *in situ* dynamics that was presented in section 5.3.3, there are a few other indicators of the trustworthiness of the proposed IBM. For instance, upon closer inspection of the average swimming speed and the average distance between c_i and $p_i(t)$, visualized in Figure 5-10a and b, respectively, it is clear that the overall patterns coming forward in these plots coincide with the ones expected taking into account the assumptions underlying the migration model and the used parameter values. The model's soundness is further confirmed by the plots in Figure 5-12 because they indicate that the variability between the *in silico* population's individuals can be pronounced. This is something which is typically observed between living organisms, irrespective of their species, sex and habitat requirements, and was also observed for pike (Chapman & Mackay 1984b, Jepsen et al. 2001, Koed et al. 2006, Vehanen et al. 2006).

However, the validation also indicates that the assumed home range extent from March to May and in summer is too small. This should and can easily be adjusted in future modelling using the IBM proposed here. Further, the results of chapter 6 indicate that the model could be improved by defining the values of α and β by the water temperature instead of the date. Besides, it has been observed that the average simulated pike density near SG₃ is only one-third of the average densities recorded near SG₁ and SG₂, which is in line with expectation since the former is shielded from migrating pike by SG₂ that is encountered first by upstream migrating individuals. Naturally, it is likely that pike nonetheless might prefer to migrate to SG₃ if the carrying capacity near SG₂ is exceeded. Yet, this would require insight into the spatial distribution of this carrying capacity, which can only be assessed if one has precise and detailed knowledge on the spatio-temporal distribution of prey fish across the river Yser. We agree that the distribution of prey fish might be an important factor influencing pike migration, but data on such distributions are lacking to this day. Firstly, since it was practically not possible, nor fitting within the scope of the telemetry study to tag and position pike prey species. Secondly, existing gill net and electro fishing data sets on the fish communities in the river Yser are incomplete, such that they cannot be combined with the telemetry data set, or be used to investigate the effect in a multivariate analysis or ANOVA. Furthermore, there is no information on the diet of pike in the river Yser, which would be needed to gain insight into this species' diet that is known to vary seasonally and between water systems and even within the population (Flinders & Bonar 2008). Finally, to our knowledge there are no studies on the spatial predation behaviour of pike, which can be attributed to the fact that most studies on pike's predation behaviour are conducted within the scope of biomanipulation and because such studies would be very time consuming (Beaudoin et al. 1999, Craig 1996, Kahilainen & Lehtonen 2003).

CHAPTER 6

Adult pike movement and migration

6.1 Introduction

Pike requires diverse habitats to successfully survive and reproduce, and therefore regularly migrates, specifically during the spawning season (Casselman & Lewis 1996, Craig 2008, Knight et al. 2008, Koed et al. 2006, Ovidio & Philippart 2003, Vehanen et al. 2006). Consequently, insight into pike migration and the environmental variables that affect migration is needed for effective conservation and rehabilitation or restoration of the species. Most of the studies that have been devoted to pike movement thus far analysed patterns of displacement (Burkholder & Bernard 1994, Cook & Bergersen 1988, Diana 1980, Jepsen et al. 2001, Kobler et al. 2008a). The few studies on pike migration have focused on sedentary versus active behaviour, and have evaluated the periodicity of migration (Koed et al. 2006, Masters et al. 2003, Vehanen et al. 2006).

Thus far, little is known about the environmental factors influencing migration (Koed et al. 2006, Ovidio & Philippart 2003). It is assumed that migration to spawning grounds is initiated by high flows after ice-out (Craig 1996) and is triggered by an increase of water temperature (Ovidio & Philippart 2003). Nothing is known about the effect of diel temperature change on migration and a potential time lag between migration and water temperature or flow. Furthermore, it is possible that these effects differ between latitudes. This study is unique in the sense that it investigates the relation between diel water temperature change and migration, and that it accounts for potential effects of the location where the pike were observed. Beside Masters et al. (2003) this is the only study investigating this in a lowland river at lower latitudes. In addition to Masters et al. (2003) this river is characterized by anthropogenic impacts.

The aim of this chapter on pike movement and migration was to identify the occurrence of adult pike migration and which environmental variables influenced migration. Therefore we firstly described the pattern of pike movement during one year and evaluated when migration occurred. Further, the effect of temperature, diel temperature change, flow and photoperiod on migration was analysed, taking into account sex, length and mass differences and potential

dependence on the location in the river. If certain thresholds of e.g. temperature and flow could be identified at which pike starts migrating towards spawning areas, river managers can use this information for instance to temporarily open migration barriers in the river by adjusted barrier management.

6.2 Material and Methods

6.2.1 Study area and data collection

We refer to chapter 3 for a detailed description of the study area, the environmental data used in this chapter and the collection of the pike data.

6.2.2 Data analysis

Pike movement was quantified by the minimum average daily distance moved (MDD). The MDD was defined as the distance along the midline of the river between the positions of two consecutive observations of the same fish, divided by the number of days between the observations. Data from the first two weeks after tagging were deleted, to avoid potential distortion of results following tag implantation (Beaumont et al. 2002).

To evaluate the movement patterns of the pike and identify when migration occurred, we analysed the observations from December 2010 to December 2011. The analysis on the environmental variables affecting migration only included data from December 2010 to May 2011. MDD values were not normally distributed (Shapiro-Wilk p -value: 2.62156×10^{-39}) and were $\log(x+1)$ -transformed.

We analysed the impact of eight different variables on pike migration: the water temperature, which is the average of one day at three locations in the study area (Figure 3-3), the dial (24 h) water temperature change, which is the difference in temperature between consecutive days, flow, the location in the study area where pike were observed, the photoperiod, mass, length and sex. However, initial data exploration (following Zuur et al. 2009) showed strong collinearity based on the variance inflation factor (VIF) between length and mass and between photoperiod and water temperature (Table 3-6), and length and photoperiod were thus omitted from further analysis. To avoid loss of information by removing length, we evaluated a potential effect of pike length, but no significant effect was found during backward selection in the GAM (t -value= 1.35, $p = 0.18$).

To investigate the impact of temperature and flow on migration, these variables were included in the analysis, but we also evaluated if a time lag existed between peaks in pike migration, defined as the MDDs exceeding the 85% percentile of the MDDs per individual, and peaks in water temperature and flow. Specifically, we analysed the impact of temperature and flow over time lags of 1 to 5 days by defining the cumulative temperature and flow over these time lags. Since these variables were highly correlated with the water temperature and flow (Table 3-6), we did not include the cumulative temperature and flow in the further analysis.

Since a full model with the remaining six covariates and all their interactions would still be too complex, we first evaluated whether all covariates and interactions are expected to have a significant effect on the MDD (Zuur et al. 2009). We found that pike mass did not significantly explain the remaining variance in the residuals of a LM containing all selected covariates beside mass, while other covariates did ($F = 1.77$, $df = 1$, $p = 0.18$). Therefore we omitted mass from further statistical analysis. Based on our ecological knowledge and interest, we evaluated whether the effect of temperature and flow on MDD differed between sexes, whether the effect of temperature on MDD depended on flow and vice versa, and whether the effects of temperature and flow differed according to the location of the

individual in the study area. Consequently, we started model development with five covariates and five two-way interactions in the basic full model F1:

$$\text{LogMDD}_i = \alpha + \beta_{1i} * \text{water temperature}_i + \beta_{2i} * \text{diel water temperature change}_i + \beta_{3i} * \text{flow}_i + \beta_{4i} * \text{location}_i + \beta_{5i} * \text{sex}_i + \beta_{6i} * \text{water temperature}_i * \text{sex}_i + \beta_{7i} * \text{flow}_i * \text{sex}_i + \beta_{8i} * \text{water temperature}_i * \text{flow}_i + \beta_{9i} * \text{water temperature}_i * \text{location}_i + \beta_{10i} * \text{flow}_i * \text{location}_i + \varepsilon_i$$

where α is the intercept, β_{ji} are the covariate coefficients, j is the index of the covariate and i is the i^{th} record in the dataset. To investigate how these variables and interactions affected pike migration different models were fitted to the data: a linear model (LM), a general additive model (GAM), a general linear mixed model (GLMM) and a general additive mixed model (GAMM). Models were compared using the Aikake information criterion (AIC) and autocorrelation was evaluated using the autocorrelation function (ACF). All analyses were conducted using the nlme and mgcv libraries in R (Hastie & Tibshirani 1990, Wood 2006). Starting from the full model (F1) we firstly investigated the addition of a random part to F1. We analysed the effect of adding individual pike as a random intercept and extended this with random slopes for temperature, diel temperature change, flow and location. Adding individual pike as random intercept substantially reduced the autocorrelation between consecutive observations. Specifically, in the LM (M1 in Table 6-2) autocorrelation was found between 10 consecutive observations, whereas this was reduced to correlation between only 3 consecutive observations when individual pike was added as a random intercept (M2 in Table 3-7). The GLMM with individual pike as random intercept and water temperature as random slope performed best.

Further exploration of the GLMM residuals indicated the need for non-parametric smooth functions to better describe the effects of the numeric covariates. The GLMM was therefore extended to a GAMM (M6 in Table 3-7), and analogous the LM was extended to a GAM (M3 in Table 3-7). In both models (M6 and M3) a model selection was performed that led to M4 and M7, respectively. The difference existed in the smoothing function on water temperature and flow that contained two smoothers (one for each sex) in the GAM (M4 in Table 3-7), whereas this was only one for temperature and none for flow in the GAMM (M7 in Table 3-7). Although the autocorrelation between consecutive observations in the GAM was higher, it had a lower AIC than the corresponding GAMM (Table 3-7). Therefore, the GAM (M4, Table 3-7) was selected as the final model.

$$\text{LogMDD}_i = \alpha + f_{1i}(\text{water temperature}_i * \text{sex}_i) + \beta_{2i} * \text{diel temperature change}_i + f_{2i}(\text{flow}_i * \text{sex}_i) + f_{3i}(\text{location}_i * \text{sex}_i) + \varepsilon_i \quad (\text{M4})$$

Table 6-1: *P*-values of the F-statistic for two linear regression models: one model with all 9 covariates (initial model) and one model without the covariates having a high collinearity (reduced model), and the variance inflation factor (VIF) values for the initial model. In the initial model, pike minimal daily distance moved (MDD) is modelled as a function of the covariates listed in the first column. Sex is not included because this is a discrete covariate. In the second and third columns, the *p*-values and VIF values for the initial model are presented (note that no covariates have been removed yet). In the fourth column *p*-values are presented for the model after collinearity has been removed by sequentially deleting each covariate for which the VIF value was highest until all remaining VIFs were below 3. The initial and reduced model differed significantly (*p*-value: 0.012).

Covariate	<i>p</i> -value (initial model)	VIF	<i>p</i> -value (collinearity removed)
Water temperature	0.308	38.645	0.311
Water temperature with time lag	0.008	40.429	removed 1 st
Diel water temperature change	0.838	2.638	0.054
Flow	0.012	8.413	0.035
Flow with time lag	0.097	8.824	removed 3 rd
Pike mass	0.339	26.081	0.332
Pike length	0.115	26.184	removed 2 nd
Photoperiod	0.068	7.475	removed 4 th
Location where pike were observed	0.000	1.038	7.833×10^{-5}

Table 6-2: Comparison of alternative models describing the effect on pike minimal daily distance moved (MDD) of water temperature, flow, diel water temperature change and the location where pike were observed, and their interaction with sex .

Model	Model description	-log-lik	df	AIC
M1	LM on F1	-1530.822	12	3085.644
M2	GLMM on F1 with individual as random intercept and water temperature as random slope	-1487.852	15	3005.704
M3	GAM on F1	-	31	2860.367
M4	GAM on reduced F1, two smoothers on water temperature, two on flow and two on location	-	27	2854.239
M5	GAM on reduced F1, one smoother on water temperature, none on flow and one on location	-	16	2868.262
M6	GAMM on F1 with random part of M2	-1455.660	15	2941.320
M7	GAMM on reduced F1 with random part of M2, one smoother on water temperature, one on flow and one on location	-1428.292	11	2878.584

Models were compared using the Aikake information criterion (AIC). All analyses were conducted using the nlme and mgcv library in R (Hastie & Tibshirani 1990, Wood 2006). -log-lik: log likelihood ratio, df = degrees of freedom.

6.3 Results

6.3.1 Annual movement

The estimated MDDs differed significantly between different months ($F = 12.5$, $df = 11$, $p = 2.2 \times 10^{-16}$). Specifically, the MDD (minimum average daily distance moved) was highest during February and March (Figure 6-1). Overall, pike migrated less than 500 m day⁻¹ for most of the time (75 %) and only sporadically moved distances up to 2000 and 4000 m day⁻¹ (Figure 6-1 and Figure 6-3, Table 3-3).

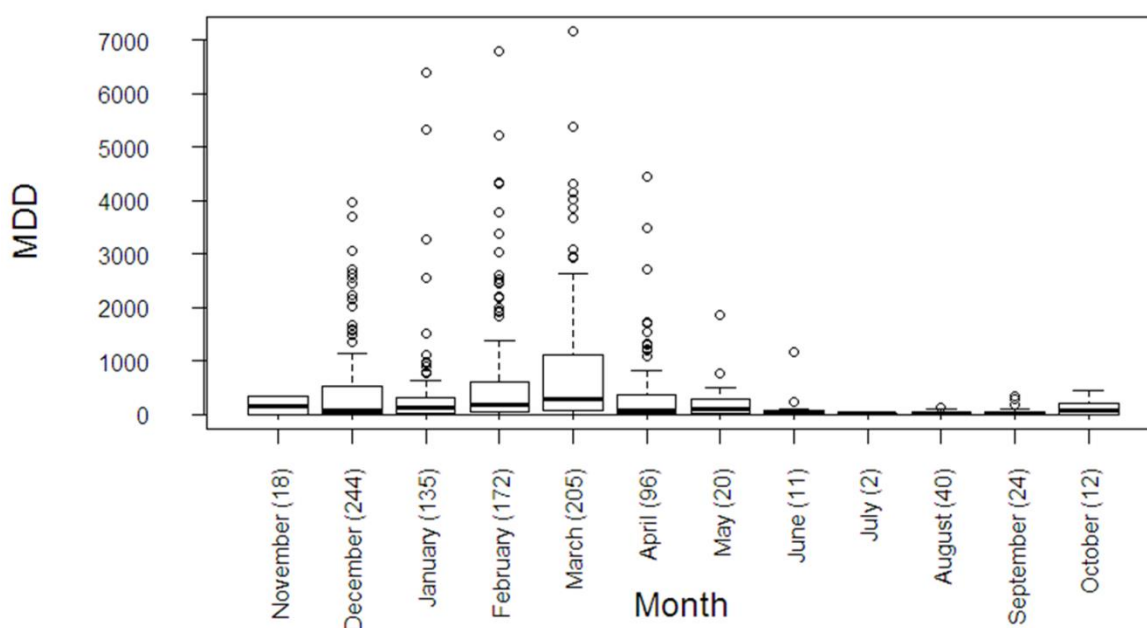


Figure 6-1: Boxplots of the minimal daily distance moved (MDD) for 12 pike per month. The numbers in the x-axis indicate the number of pike observations per month. (bold vertical line: average, whisker: minimum and maximum without outliers, circle: outlier).

6.3.2 Migration

About 75 % of the distances longer than 2000 m day⁻¹ were travelled during February and March. Two female pike and one male never swam more than 1000 m day⁻¹ (Table 3-3, Figure 6-3B, C, and G).

During February and March, eight pike migrated to locations that were distinct from the locations where they resided most of the year in the river (Figure 6-3 and Figure 6-4). At least three of these migrated to two smaller upstream tributaries where YOY pike were found during the YOY fishing campaign. The male pike that never moved farther than 1000 m day⁻¹ was one of these. This indicates that migration to a spawning area does not necessarily entail a longer distance (Figure 6-3 and Figure 6-4).

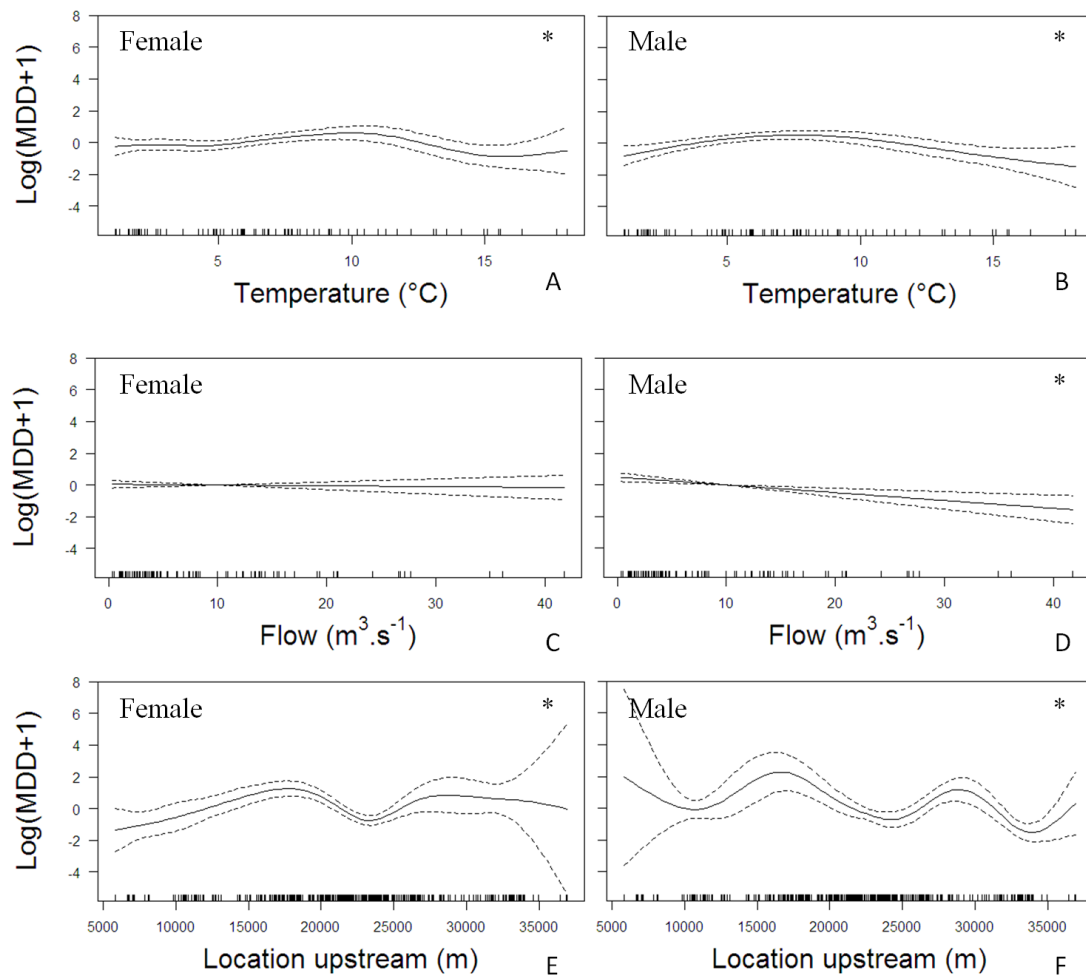


Figure 6-2: Smoothers and 95% point wise confidence intervals of model M4 (A to F), illustrating the non-linear relations between log (MDD+1) and water temperature (A, B), flow (C, D) and location where pike were observed (E, F) for male and female pike. Significant relations are marked by an asterics. (A: $p = 0.0034$, B: $p = 0.0001$, C: $p = 0.3079$, D: $p = 0.0003$, E: $p = 3.62 \times 10^{-10}$, F: $p = 2.46 \times 10^{-9}$).

6.3.3 Triggers for pike migration

Four environmental variables significantly affected pike migration, ranging from the location where pike were observed (strongest effect), over water temperature and flow to diel water temperature change (weakest effect). The MDD increased when the water temperature rose to 9-10 °C, above which it tended to decrease again (Figure 6-2). Specifically, male pike MDD increased with rising water temperatures between 0 °C and 8 °C, whereas female pike MDD only increased at temperatures above 5 to 6 °C, till 10 °C (M4: $F_{\text{females}} = 3.21$, $p_{\text{females}} = 0.003$, $F_{\text{males}} = 5.97$, $p_{\text{males}} = 0.000$, Figure 6-2). The relation between the MDD and the diel temperature change was positive (M4: estimated coefficient = 0.27 ± 0.11 , $t = 2.56$, $p = 0.011$). Furthermore, the MDD slightly decreased with increasing flow. The male pike MDD decreased slightly more with rising flow than the female pike MDD (M4: $F_{\text{females}} = 1.20$, $p_{\text{females}} = 0.308$, $F_{\text{males}} = 13.23$, $p_{\text{males}} = 0.000$, Figure 6-2). Our initial data exploration indicated that this correlation was even more negative above flows of $20 \text{ m}^3 \text{ s}^{-1}$. This was not found after model selection, which indicated a linear relationship between MDD and flow.

The MDD was also significantly related to the location in the study area, being low between 22 and 25 km upstream, and higher both upstream and downstream of this location (M4: $F_{\text{females}} = 8.53$, $p_{\text{females}} = 3.62 \times 10^{-10}$, $F_{\text{males}} = 7.17$, $p_{\text{males}} = 2.46 \times 10^{-9}$, Figure 6-2).

Model selection revealed that the interactions between the environmental variables and location in the study area were insignificant. Specifically, the significant relationship between pike MDD and location in the study area does not mean that the pike's reaction to temperature and flow depended on their location. Although the location in the study area appeared to have the strongest impact on MDD, this does not imply that location is triggering migration.

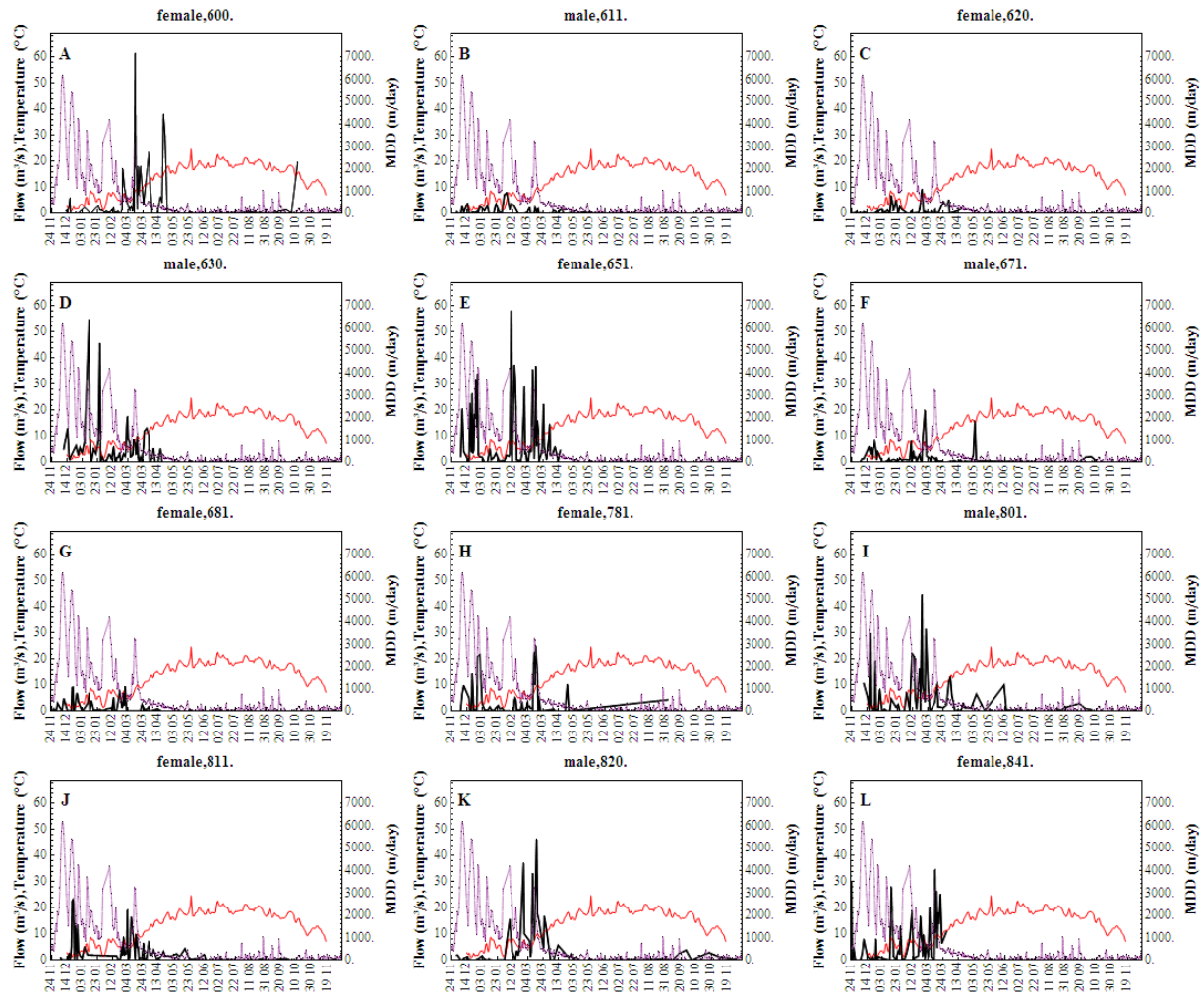


Figure 6-3: Water temperature (red) and flow (purple) versus minimal daily distance moved (MDD) (black) of 12 pike (A to L). X-axis labels are based on day (d) and month (m) as follows: ddmm. Sex and the three last numbers of the fish ID are indicated at the top of each graph.

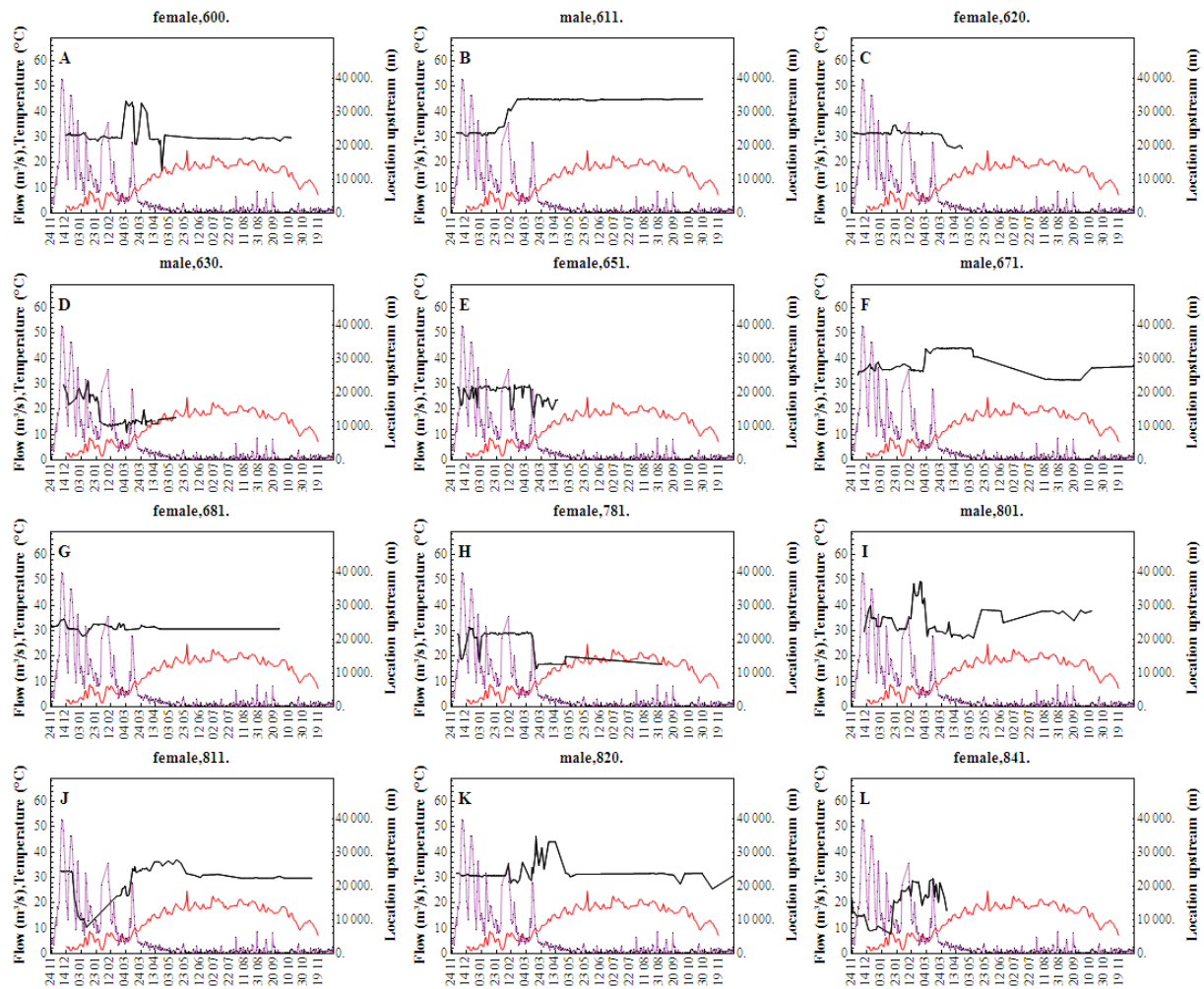


Figure 6-4: Location where pike were observed (black) versus water temperature (red) and flow (purple) of 12 pike (A to L). X-axis labels are based on day (d) and month (m) as follows: ddmm. Sex and the three last numbers of the fish ID are indicated at the top of each graph.

6.4 Discussion

Pike MDDs were highest between December and May with a peak in February and March. Higher MDDs from December to February could be explained by a high competition for food during these months (Chapman 1968, Dawson et al. 1991, Knight et al. 2008), whereas higher MDDs between February and May could coincide with the spawning migration, which is often observed to encompass longer distances compared to the distances moved during the rest of the year (Koed et al. 2006, Ovidio & Philippart 2003). The higher MDDs in February and March correspond with earlier observations by Koed et al. (2006) and Knight et al. (2008). Cook and Bergersen (1988) reported a higher pike activity during April and May and the lowest activity during October. In contrast, Kobler et al. (2008b) and Vehanen et al. (2006) both reported a higher pike activity from the beginning of June to September and a lower pike activity from December to March and from October to April, respectively, whereas Baktoft et al. (2012) observed no consistent seasonal trend in pike activity.

Our analysis on the relation between environmental variables and migration revealed that four environmental variables significantly affected pike migration, ranging from the location where pike were observed (strongest effect), over water temperature and flow to the diel water

temperature change (weakest effect). Specifically, the relation between the location where pike were observed and the MDD revealed a lower MDD in an area between 22 and 25 km upstream of the tidal sluice. This may suggest a preference of pike for this specific area or habitat type. The area is characterized by a semi-natural riparian habitat, which is assumed to be the most suitable habitat type available. Other characteristics such as river morphology or prey densities may also affect the low MDDs in this area, but this was not further investigated in this study. Despite the significant relation between the location where pike were observed and the MDD, this location had no significant influence on the relations between temperature and MDD, and flow and MDD.

The relation between water temperature and MDD showed an increase of MDD with rising temperatures until maximally 10 °C, above which MDD decreased again. This corresponds with the assumption that pike spawning migration is stimulated by rising temperatures (Craig 1996, Lucas et al. 2001, Ovidio & Philippart 2003) and is in line with the analysis of Lucas et al. (1992), who found highest daily pike movement between 8 and 10 °C. In the study of Ovidio et al. (2003), pike started the upstream migration at temperatures between 6.7 and 8.7 °C. We hypothesize that 9 to 10 °C is a threshold level for migration in our study, since the activity was highest at ca. 9 °C and there was only a one-day time lag between migration peaks and temperature peaks exceeding 10 °C. The decrease of MDD at temperatures above 10 °C, could indicate that pike have arrived at their spawning area by then. Although we could not observe spawning after migration, the occurrence of YOY pike at two locations visited by tagged pike suggests that at least some tagged pike visited habitats that are most likely to be suitable for spawning.

The different effect of water temperature on MDD of male versus female pike found in our study indicates that male pike are triggered to migrate at lower temperatures than female pike. Male pike MDDs increased when temperature exceeded 0 °C, while female pike MDDs only increased when temperature exceeded 5-6 °C. Craig (1996) also reported that males started spawning migration earlier than females.

The relation between diel water temperature change and MDD was linear and indicated that the MDD slightly increased with increasing diel water temperature change. This relation was however less significant than the relation between MDD and water temperature, which may indicate that water temperature more strongly affects pike migration than the diel temperature change.

Although Craig (1996) demonstrated that migration was triggered by increased flow, we observed a negative relation between MDD and flow. This discrepancy may be because the water velocity in the River Yser often exceeded the critical velocity that inhibits pike movement during the study period (Jones et al. 1974).

Sex had no significant effect on pike MDD and only affected the relations between MDD and water temperature, flow and the location where pike were observed. The insignificant relation between sex and MDD is in line with the study of Burkholder and Bernard (1994), but contrasts with the observation of sex-dependent movement rates by Lucas (1992) and Koed et al. (2006). Lucas (1992) observed a higher activity of males, whereas Koed et al. (2006) found a higher activity of females. The dissimilarity of the discussed studies is notable and was also observed in studies on pike's diurnal activity, on the grouping of pike into sedentary and active animals and on the pike length-movement rate relation. As Kobler et al. (2008b) and Jepsen et al. (2001) already stated, these differences might not only reflect variation in pike behaviour among different ecosystems, but also differences in method and study design. In this respect, we suggest the most important differences between our study and the aforementioned pike telemetry studies are the shape (lake versus river) and the length of the study area, beside the statistical method applied compared to the migration studies. Comparable to the aforementioned studies we also studied between 5 and 40 pike. We tracked

the pike for one year at different sampling intervals, which is comparable to the protocols of the aforementioned studies on pike in rivers (Koed et al. 2006, Ovidio & Philippart 2003, Vehanen et al. 2006) but contrasts with most of the studies in lakes, specifically with those of Diana (1980) and Baktoft (2012), in which pike were tracked at equal, short time intervals over 50 days and 2 years, respectively. Apparently, the tracking protocols in radio telemetry are highly dependent on the shape and extent of the study area. Continuous monitoring of tagged fish to a few meters precise using acoustic telemetry and stationary radio receivers is only possible in a small lake. Consequently, the sampling intervals are larger and more variable in telemetry studies on rivers, specifically on large river systems.

The study of Baktoft et al. (2012) indicated that long sampling intervals may entail a great sampling error. This is also applicable on our study, even though this sampling error was minimized by only lowering the tracking frequency when reduced activity was observed. For instance, pike were observed to be less active from May to November, so sampling error is expected to be relatively low in this period, even though our tracking frequency was lowered (Cook & Bergersen 1988, Knight et al. 2008, Koed et al. 2006). Our study area entailed > 60 km of accessible river channels, whereas this was between 2 and 30 km in other studies (Koed et al. 2006, Masters et al. 2003, Ovidio & Philippart 2003, Vehanen et al. 2006). In a study area of this size it is practically difficult to track more than 15 pike at equal small (daily) sampling intervals for more than one season. This is also indicated by the number of studied animals in other radio telemetry studies. For instance Koed et al. (2006) who studied 10 pike and Ovidio and Philippart (2003) who studied 6 pike. We suggest that studies with a similar approach therefore combine periods of high (daily) tracking frequency with periods of lower (weekly) tracking frequency or apply more sophisticated approaches to allow detailed tagging of a high number of pike in a large study area.

The lack of complete certainty on the occurrence of spawning after migration was encountered as a limitation here to exclusively investigate the triggers for spawning migration. To overcome this problem, future research on the triggers of migration could be expanded by an identification of the true purpose of each migration. For instance, accelerated failure time or Cox regression (Castro-Santos & Haro 2003) could be applied to analyse the triggers for spawning migration. Besides, it could reveal how many individuals of the population spawn and migrate to spawn, and how many spawning migrations occur per individual during one spawning period.

Based on our results river managers could consider the impact of water temperature on pike migration to facilitate accessibility of small tributaries and spawning grounds, e.g. by opening valves at water temperatures between 0 and 12 °C in spring. Hence, pike are not blocked from suitable spawning habitat prior to spawning and are not trapped in small tributaries after spawning. The apparent inhibition of pike migration at high flows suggests that pike could benefit from the buffering of peak flows, e.g. by restoring floodplains and increasing lateral connectivity. An increased lateral connectivity may allow pike to enter side arms, avoiding high flows in the main river channel. Our study not only provides further insight into pike migration, but also presents a statistically underpinned approach to analyse the complex non-linear relation between environmental variables and fish migration in general. This information may be crucial for effective conservation worldwide and to evaluate management actions, such as the restoration of connectivity to spawning habitat. For instance, similar research on the effect of temperature and flow on the spawning migration of other fish species, combined with the results found here, could indicate the water temperature or flow frame in which free fish migration is most effective.

CHAPTER 7

Adult pike habitat use and preference

7.1 Introduction

Loss of natural habitat by canalisation, water pollution and migration barriers caused pike (*Esox lucius* Linnaeus 1758) population declines and impedes successful rehabilitation programmes (Chapman & Mackay 1984a, Ovidio & Philippart 2003, Radomski & Goeman 2001). Indeed, pike requires natural habitats to successfully survive and reproduce, such as shallow areas with submerged vegetation to spawn and areas with emergent vegetation to hunt for prey and hide from larger cannibalistic pike (Bry 1996, Casselman & Lewis 1996, Grimm & Klinge 1996). Adult pike choose habitat according to intrinsic fitness gradients, equalizing their fitness across habitats (Haugen et al. 2006). They are versatile in their habitat use, depending on availability of prey and other factors (Chapman & Mackay 1984b). Although they use the open water as well as vegetated areas, they are more often observed in the proximity of vegetated areas than would be expected if they were choosing the habitat randomly (Chapman & Mackay 1984a). Studies on the impact of river and lake management on pike have mainly focused on juvenile and spawning habitat requirements (Cooper et al. 2008, Engstrom-Ost et al. 2005, Farrell et al. 1996, Hawkins et al. 2003, Miller et al. 2001, Skov & Berg 1999, Skov et al. 2002, Skov et al. 2003a).

The studies that revealed adult pike behaviour were mainly conducted in natural to semi-natural lake (Chapman & Mackay 1984a, Cook & Bergersen 1988, Diana et al. 1977, Haugen et al. 2006, Kobler et al. 2008a, Kobler et al. 2008b) and river (Masters et al. 2003, Vehanen et al. 2006) systems. However, a gap still exists for river systems characterised by an artificial environment. Large pike may use the whole river or lake, including the most impacted areas, or restrict their home range to the least impacted areas. Furthermore, they may use artificial riparian habitats or avoid them. The only study that compared an impacted habitat to a less impacted habitat was conducted in a reservoir and a lake (Jepsen et al. 2001). Although large behavioural differences were observed between the reservoir and the lake, the study revealed more variation between individuals within each population. Insight into the required physical

and ecological habitat conditions of adult pike in a modified river system can further improve the effectiveness of river conservation and rehabilitation plans.

Therefore in this chapter we aimed to investigate adult pike habitat use and preference in a river characterised by an artificial environment. Specifically, we evaluated which river parts were used at the macro-scale and which riparian habitat types were used and preferred at the meso-scale, based on the radio telemetry data. These results also provided insight into the impact of riparian habitat rehabilitation on adult pike and may be used to more efficiently manage pike rivers, e.g. by enhancing the lateral connectivity with river side arms or by reconstructing natural riparian habitats.

Further in this thesis we define habitat rehabilitation as an enhancement of the habitat without the aim to go back to the original state. Habitat restoration is defined as restoration with the aim to go back to a defined natural or historical reference situation.

7.2 Material and methods

7.2.1 Study area

We refer to chapter 3 for a detailed description of the study area, the environmental data used in this chapter and the collection of the pike data.

7.2.2 Data analysis

The smallest scale at which variation in the defined riparian habitat types occurred was 20 m. Consequently, the riparian habitat use and preference was assessed by dividing the banks of the main river, the tributaries and side arms in segments of 20 m length. For segments consisting of more than one riparian habitat type, the habitat type that covered more than 50% of the segment was selected. The riparian habitat type within each segment was determined based on riparian habitat data retrieved from a digital map (INBO, unpublished data) in ArcMap (ArcGIS 10, ESRI BeLux). Riparian habitat use and availability were defined as the number of segments used and available, respectively.

Habitat use at the macro-scale was evaluated by counting the pike observations in the river, tributaries and side arms. At the meso-scale, the compositional analysis as proposed by Aebischer et al. (1993) was applied to find evidence for riparian habitat preference and to investigate riparian habitat use. Since we had no information on the occurrence of territoriality within the pike population (Skov & Koed 2004) and a potential different habitat availability per individual (Aebischer et al. 1993), habitat use and preference was evaluated at three levels of habitat selection (further named orders of habitat selection according to Johnson 1980). The three orders differed in the quantification of used and available habitat. In the first order analysis the used and available habitats in the whole study area were considered. The second order analysis considered the used habitat in the home ranges and the available habitats in the whole study area, whereas the third order analysis analysed the used and available habitats within each pike home range (Aebischer et al. 1993). Consequently, comparison of the first and third with the second order analysis allows evaluating a different definition of habitat use (here pike observations versus pike home ranges), whereas the comparison of the first and second order analysis with the third order analysis allows evaluating a different definition of habitat availability (here availability in the whole study area versus availability within the home range). Home ranges were calculated using the Brownian Bridge Kernel (BBK; Horne et al. 2007; Figure 7-1) and all home ranges were stable.

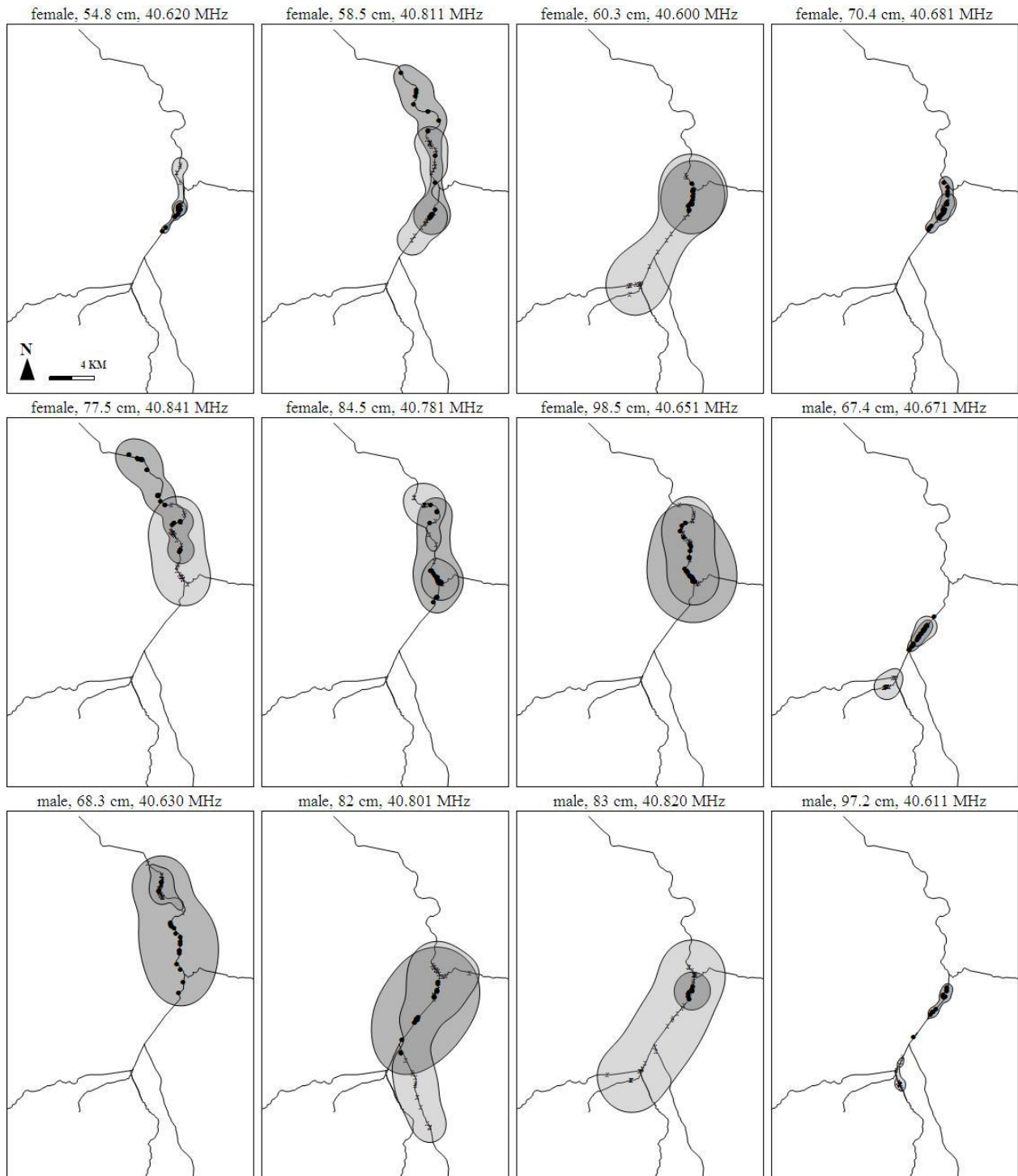


Figure 7-1: Home ranges and observations of 12 pike in winter (dark grey polygon and black dots, respectively) and spring (light grey polygon and black x, respectively). Home ranges are 95% Brownian Bridge Kernel (BBK) home ranges. Sex, body length and pike ID are indicated on top of each graph.

To investigate habitat use the riparian habitat types were ranked according to their relative use, from 'most used' (top) to 'least used' (bottom). Ranking the riparian habitat types overcomes the problem of dependence between habitat types (Aebischer et al. 1993). Although the aforementioned analysis (Aebischer et al. 1993) allows testing the relative habitat use and the occurrence of riparian habitat preferences, no absolute preference per

riparian habitat type is calculated. Therefore, we calculated selection ratios and their associated Bonferroni-adjusted 95% confidence intervals as proposed by Rogers & White (1990) in addition to the analysis proposed by Aebischer et al. (1993). The selection ratio pools observations from all fish in the sample, but takes variation in resource selection from individual fish into account (Manly 2002, Manly et al. 1993). When a selection ratio and accompanying CI is higher than 1.0, habitat preference is considered significant (Hobbs & Bowden 1982, Manly 2002, Manly et al. 1993, Rogers & White 1990). The selection ratios and CIs were calculated for each pike individual (\hat{w}_{ij}) and for the population (\hat{w}_i). The selection ratio per individual pike was calculated as follows:

$$\hat{w}_{ij} = u_{ij} / (\pi_i u_{+j}),$$

where u_{ij} is the number of segments of habitat type i used by fish j , u_{+j} is the total number of segments used by fish j and π_i is the availability of riparian habitat type i defined as the ratio between the number of segments of habitat i and the total number of segments in the study area between the most upstream and most downstream pike observation (Manly 2002, Manly et al. 1993). Similarly, the selection ratio for the population was calculated as follows:

$$\hat{w}_i = u_{i+} / (\pi_i u_{++}),$$

where u_{i+} is the number of segments of habitat type i used by all fish and u_{++} is the total number of segments used (all riparian habitat types by all pike). The CIs were defined by the standard error ($SE(\hat{w}_i)$), which was calculated as follows:

$$SE(\hat{w}_i) = \sqrt{\frac{n}{(n-1)(u_{++})^2} \sum_{j=1}^n \left(\frac{u_{ij}}{\pi_i} - \hat{w}_i(u_{+j}) \right)^2},$$

where n is the number of pike. The selection ratio for each riparian habitat type was evaluated at the 95% confidence level and the CI was calculated respectively as:

$$CI = \hat{w}_i \pm z_\alpha SE(\hat{w}_i).$$

Consequently, z_α was 1.65, corresponding to an upper tail probability of 95%.

To statistically test for individual differences in riparian habitat preference, the log-likelihood test statistic (χ^2_{L1}) was used:

$$\chi^2_{L1} = 2 \sum_{j=1}^n \sum_{i=1}^I u_{ij} \log_e \left[\frac{u_{ij}}{\left(u_{i+} u_{+j} / u_{++} \right)} \right].$$

If the value of χ^2_{L1} is sufficiently large with $(I-1)(n-1)$ degrees of freedom, there is evidence that pike riparian habitat preference differs between individuals (Rogers & White

1990). All statistical tests consider individuals as sampling units and do not pool data across individuals. All statistical analyses were conducted for winter and spring.

All analyses were performed in R (R Development Core Team 2008) and the package *adehabitat* 0.3.8 (Calenge 2006) was used to perform the compositional analysis and estimate the home ranges.

7.3 Results

7.3.1 Habitat use at the macro-scale

The use of the main river was similar in winter and spring, whereas the use of the tributaries and side arms differed substantially. In winter, 70% of all pike observations were located in the main river. The river was used by all pike and two pike were even always observed there. The other nine pike were observed there between 25 and 95% of the observations and regularly moved in and out of the main river (Figure 7-2). Although six side arms were available in the study area, only S1 and S2 were used (Figure 3-3) and thus pike did not use any of the four artificial side arms. Five pike used both side arms and two used only S1. Based on all observations in winter, pike used the side arms relatively more (26% of the observations) than the tributaries (T1 and T2, 4% of the observations) and the side arms were used by more individuals (7) than the tributaries (3).

In spring, 73% of all observations were located in the main river. All pike used the main river and two individuals were never observed outside the main river. Again only the two natural side arms were used. Some pike also used two small tributaries upstream in the study area (T3 and T4, in total 15% of the observations), beside the larger tributaries (T1 and T2). In contrast to winter, the large tributaries (T1 and T2) were used more intensely (10% of the observations) than the two natural side arms (S1 and S2; 3% of the observations). In line with winter, the artificial side arms were not used in spring. The lower use of the side arms in spring was due to six individuals that moved to the tributaries (Figure 7-2).

One individual migrated to a small tributary (T3) through a temporally opened flap gate and appeared to be locked in the tributary. All pike that used T4 had returned to the river by the end of April. The only locations in the study area where YOY were observed were T3 and T4 and specifically the tributaries of T3 and T4, which are between 0.20 and 0.40 m deep and vegetated.

At the macro-scale, the use of the river, tributaries and side arms substantially differed between individuals. Throughout winter and spring, one pike never used tributaries and side arms, another never used side arms and one fish never used tributaries. Three fish used the main river, the large tributaries and the natural side arms and only one fish used the main river, the large and small tributaries and the natural side arms (Figure 7-2).

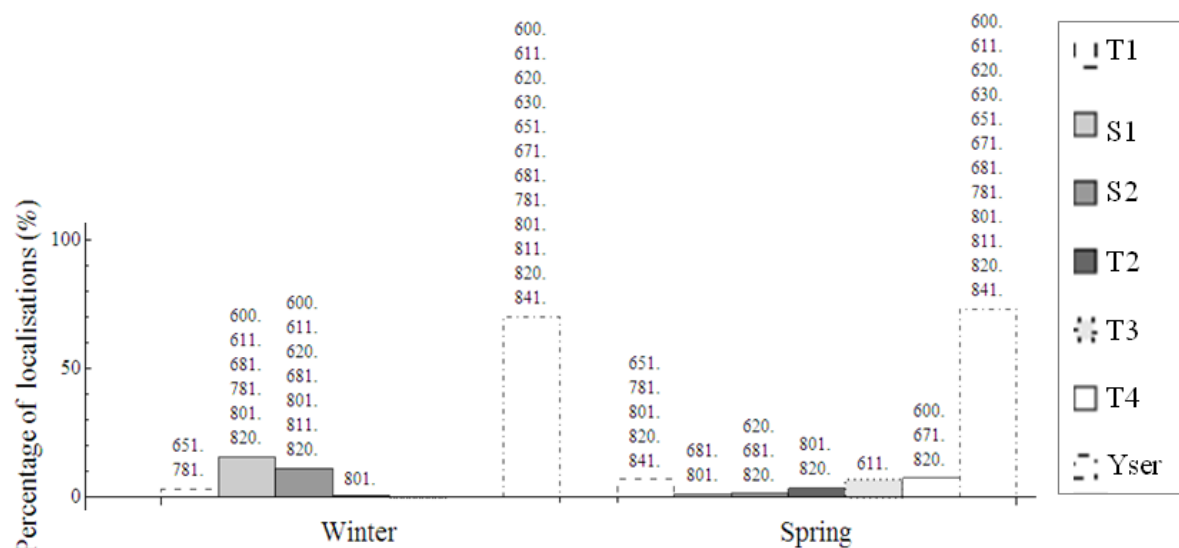


Figure 7-2: Percentage of localisations in the river Yser, its tributaries and river side arms in winter and spring (T1 = Handzamevaart, T2 = Canal from the city of Ieper to the River Yser, T3 = Landdijkgracht, T4 = Boezingegracht, S1-S2 = natural river side arms). Fish IDs (Table 3-3) above each bar indicate the observed individuals.

7.3.2 Habitat use at the meso-scale

In winter, pike used reedy and bare semi-natural banks the most and significantly more than other riparian habitats at the first and third order (Table 7-1). At the second order, reedy and woody semi-natural banks were used significantly more than other riparian habitat types (Table 7-1). In none of the orders of habitat selection it was indicated that pike often used artificial vertical banks and artificial foreshores.

Habitat preference in winter was only significant at the first order habitat selection (p -value = 0.0007), and not at the second (p -value = 0.1180) and third order (p -value = 0.1959). The selection ratios and accompanying CIs revealed that pike significantly preferred reedy semi-natural banks in winter (Figure 7-3). In contrast to their relative high use, bare semi-natural banks were not preferred (Figure 7-3). Based on the selection ratios, the absence of a significant preference for artificial vertical banks and artificial foreshores is in line with the relative low use of these riparian habitat types.

In spring, pike used reedy semi-natural banks significantly most, followed by bare semi-natural banks in all orders of analysis. Bare artificial vertical banks were significantly used more than other riparian habitats at the first and third order analysis, but not at the second order (Table 7-1). Similar to winter, the use of artificial foreshores was relatively low.

As in winter, significant habitat preference was only observed at the first order analysis (p -value = 0.0011), and not at the second order (p -value = 0.0606) and third order (p -value = 0.0980). The selection ratios and accompanying CIs revealed that pike significantly preferred bare artificial vertical banks in spring. In contrast to the significant high use of reedy semi-natural banks, no significant preference for this riparian habitat type was observed (Figure 7-3).

At the meso-scale, the preference for the riparian habitat (calculated at the first order) differed significantly between individuals in both winter (Chi-square: 130.01, df: 84, p -value: 0.0010) and spring (Chi-square: 135.63, df: 84, p -value: 0.0000). The individual variation was the largest for those habitat types that were least available, such as woody semi-natural banks and bare artificial foreshores in winter (Figure 7-3a and c) and the woody habitats (woody

artificial vertical banks and woody semi-natural banks), and reedy artificial foreshores in spring (Figure 7-3b and d).

Table 7-1: Rank of the riparian habitat types according to their relative use from most used (top) to less used (bottom) in winter and spring in three orders of habitat selection (Aebischer et al. 1993, Johnson 1980). Bold text indicates significance and asterics represent the number of habitat types that are significantly less used than the corresponding habitat type.

Winter		
First order	Second order	Third order
R:SNB *****	R:SNB **	B:SNB *****
B:SNB *****	W:SNB *	R:SNB ***
B:AV	R:AV **	B:AV **
W:SNB	B:SNB *	R:AF
R:AV	W:AV	R:AV
R:AF	B:AV	W:SNB
W:AV	R:AF	W:AV
B:AF	B:AF	B:AF
Spring		
First order	Second order	Third order
R:SNB *****	R:SNB *	R:SNB ***
B:SNB *****	B:SNB	B:SNB **
B:AV **	R:AV	B:AV **
W:SNB	B:AV	W:SNB
R:AV	W:SNB	R:AV
W:AV	W:AV	W:AV
B:AF	R:AF	B:AF
R:AF	B:AF	R:AF

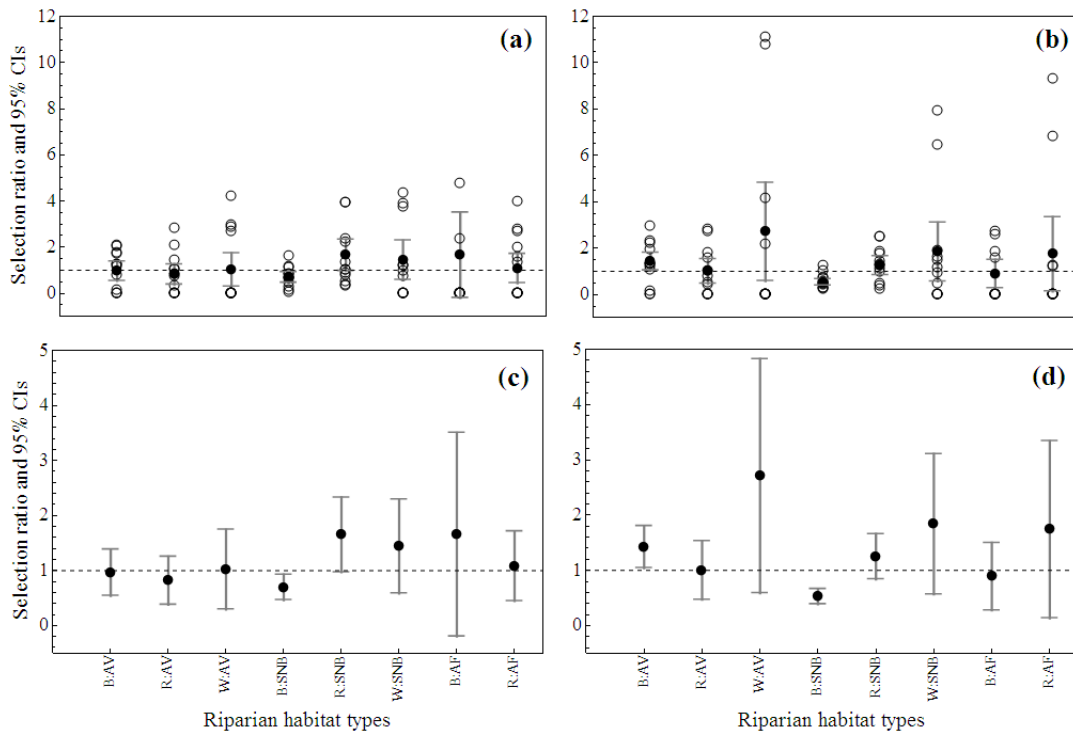


Figure 7-3: Selection ratios (on a population level: \hat{w}_i , black dots and on an individual level: \hat{w}_{ij} , white dots) and 95% confidence intervals (CIs, grey lines) for the riparian habitat types in the river Yser in Belgium (B:AV = bare artificial vertical bank, R:AV = reedy artificial vertical bank, W:AV = woody artificial vertical bank, B:SNB = bare semi-natural bank, R:SNB = reedy semi-natural bank, W:SNB = woody semi-natural bank, B:AF = bare artificial foreshore, R:AF = reedy artificial foreshore) in winter (a) and spring (b) at the first order of habitat selection. The selection ratios on a population level (\hat{w}_i) and 95% CIs were plotted on a different y-axis scale in c (winter) and d (spring).

7.4 Discussion

7.4.1 Habitat use at the macro-scale

The analysis of the macrohabitat use demonstrates that in a lowland river characterised by an artificial environment pike not only intensively use the main river, but also river side arms and tributaries. Given the large home range of eight of the 12 studied pike in winter and spring, it is not surprising that pike also used side arms and tributaries beside the main river. However, the observation that they frequented specific tributaries and side arms may suggest that these tributaries and side arms are important. Seven pike collectively used two side arms in the centre of the study area in winter, although it is known that the foraging success of pike, which is a solitary sit-and-wait predator (Craig 1996), decreases with an increasing density of conspecifics (Eklöv 1992). One hypothesis explaining why pike used the side arms and probably gave up their potential territorial behaviour (Skov & Koed 2004) is that pike look for areas of slower flowing to stagnant water to shelter from high flow. Although this hypothesis was not further investigated here, it could be supported by our analysis of the movement behaviour of the pike from this study, which revealed lower activity at high flow (Pauwels et al. 2014). Another hypothesis is that pike would leave the main river to exploit higher prey abundances. Masters et al. (2002) for instance revealed pike exploiting their prey in flooded fields and ditches in winter.

In spring, a large proportion of the observations outside the main river were situated in the small T3 and T4 tributaries upstream. Although pike spawning was not explicitly observed there, the observation of YOY indicates that spawning occurred in or near these tributaries. The YOY pike were found in tributaries of T3 and T4, which were shallower and fully covered with emergent and submerged vegetation and thus more in line with the spawning habitat requirements of pike than the habitat in T3 and T4 (Casselman & Lewis 1996, Craig 1996). Since four tagged pike invest energy in migrating 10 km upstream to these tributaries (Pauwels et al. 2014) in an energy demanding period (Diana 1983) may indicate the importance of these tributaries' habitat. However, another explanation could be homing behaviour of pike to the natal site. These observations are also supported by the observations of Koed et al. (2006) in a natural river system, demonstrating that despite suitable spawning grounds available near the areas where pike resided most of the year, several pike, mainly females, migrated to distant locations during spring.

The fact that two pike were always observed in the main river in spring could indicate that this habitat is suitable for spawning, or for pre-mature pike that have not spawned during the study period. Since spawning was not observed in our study, further research could clarify this. The observation of juvenile pike in one side arm and in one artificial foreshore in the main river in a previous study might be an indication that spawning in the main river occurs (Mouton et al. 2012a).

Our habitat use analysis at the macro-scale suggests that river managers should focus on conservation of the existing tributaries and side arms and that successful creation of new side arms may indeed be a more complex action than expected. Furthermore, the high individual variation in use of the river, tributaries and side arms emphasizes the high importance of macrohabitat heterogeneity for adult pike.

7.4.2 Habitat use at the meso-scale

The analysis on the relative use of the riparian habitats revealed that irrespective of any assumption on habitat availability or use, reedy semi-natural banks were used most and significantly more than the other riparian habitat types in both winter and spring. The higher use of reedy semi-natural banks in winter observed in this study is in line with Kobler et al. (2008b), who found a stronger association of adult pike with reed in winter than in summer. He suggests that pike follow their prey, which are less active and stay in refuges close to shore in winter. Based on literature it is also expected that pike would prefer riparian habitats that are least impacted and characterised by vegetation like reedy semi-natural banks (Chapman & Mackay 1984b, Grimm & Klinge 1996). In contrast to the semi-natural banks, artificial foreshores were never significantly used. This suggests that pike might benefit more from conservation of existing semi-natural banks than from creation of artificial foreshores.

The analyses of habitat preference revealed significant pike preference for riparian habitat types at the first order. This means that if we assume that adult pike were able to freely choose the habitat in the whole study area, without limitations like territoriality or migration barriers (Haugen et al. 2006), they significantly prefer one or more riparian habitat types. However, this contrasts with the absence of significant riparian habitat preference at the second order analysis, where the habitat use is defined based on the pike's home range. Assuming that pike habitat use was well described by the pike observations, this could result from the relatively high patchiness of the riparian habitats within the home ranges. The absence of significant habitat preference in the third order analysis means that no riparian habitat preference occurred within the home ranges either. This might indicate that pike were free to choose their home range, which is further supported by the similar rank of the riparian habitat types in the first and third order analyses.

The selection ratios revealed that pike significantly preferred reedy semi-natural banks in winter and bare artificial vertical banks in spring. These riparian habitat types were indeed also relatively often used, which might thus reflect the preference of pike for these riparian habitat types. In contrast, pike did not prefer bare semi-natural banks although they often used it. Although no significant preference for woody semi-natural habitats was observed, the higher proportion of woody semi-natural banks in the winter home ranges supports their potential importance for some adult pike. However, large individual differences in selection ratios were also observed, especially for the riparian habitat types that were ranked lower in the habitat use analysis (Aebischer et al. 1993) such as the woody riparian habitats. This is in line with previously observed differences in preference between individuals (Chapman & Mackay 1984b), but can also result from an unequal availability of these riparian habitat types to each individual due to an overall low availability in the study area.

The conclusions following from these results are similar to those from the macrohabitat analysis. The high variability in individual mesohabitat preference indicates that mesohabitat heterogeneity may be much more important for the population's welfare than previously expected and pike may benefit more from conservation of existing semi-natural banks than from rehabilitation of artificial vertical banks.

Since the number of fish that could be tracked using radio telemetry in a large study area at daily time intervals is never substantially large (Burkholder & Bernard 1994, Cook & Bergersen 1988, Diana 1980, Jepsen et al. 2001, Kobler et al. 2008a, Koed et al. 2006, Lucas 1992, Lucas et al. 2001, Masters et al. 2003, Ovidio & Philippart 2003, Vehanen et al. 2006), it is necessary to question the representativeness of the number of studied fish for the population. Population representativeness is difficult to determine and might be biased at different steps during a study. For instance the method of sampling the individuals might already bias the results, as with fyke nets it is more likely to catch mobile individuals over sedentary individuals. The representative number of studied individuals depends on the extent of the variation within the population and how well this variation is captured by the studied fish. Further research could indicate how representative 12 studied pike are for the pike population in the river Yser by investigating more individuals and by precise estimates of the population size. However, the low catch frequency during regular fish samplings of the INBO in the river Yser from 1996 to 2012 (www.vis.inbo.be), and the effort needed in this study to catch 15 adult pike already indicate a small population size. At the start of our study we caught and tagged 15 adult pike because this number was regarded the maximal number feasible to daily track by radio telemetry in this study area, which consists of more than 60 km of connected waterways. However, two pike were lost before half February and one was relocated less than 25 times. The resulting sample size of 12 pike is comparable to previous pike radio telemetry studies (Burkholder & Bernard 1994, Cook & Bergersen 1988, Diana 1980, Jepsen et al. 2001, Kobler et al. 2008a, Koed et al. 2006, Lucas 1992, Lucas et al. 2001, Masters et al. 2003, Ovidio & Philippart 2003, Vehanen et al. 2006). In two of these studies more than 15 pike were studied (Cook & Bergersen 1988, Kobler et al. 2008b).

The results of this study indicate the importance of habitat heterogeneity both at the macro- and meso-scale and suggest the adult pike population benefits more from conservation of existing suitable habitats than from the enhancement of artificial habitats by bank rehabilitation. River managers could focus on the lateral connectivity between the main river and its tributaries and side arms to conserve and optimize the heterogeneity at the macro-scale and could protect and restore riparian habitats that enables growth of emergent reed and of woody vegetation like trees and shrubs on the banks. Despite river rehabilitation efforts, our findings underline the value of least impacted, (semi)natural habitats in an anthropogenically river system. Loss of these remaining suitable habitats might threaten pike populations in

artificial environments. Therefore, the precautionary principle should be applied while managing such river systems.

CHAPTER 8

Habitat suitability model for adult pike in a lowland river

8.1 Introduction

In this chapter, we describe the integration in a habitat suitability model (HSM) for adult pike of knowledge on pike ecology from A1 publications and grey literature and data on adult pike behaviour collected in the river Yser during this study. Knowledge rules were derived from the dataset by crisp membership functions. The membership functions were based on knowledge on pike ecology and its relation to the habitat from A1 publications and books (Bry 1996, Casselman & Lewis 1996, Chapman & Mackay 1984a, b, Craig 1996, Craig 2008, Koed et al. 2006, Vehanen et al. 2006) and grey literature (De Laak & van Emmerik 2006, Inskip 1982). The resulting knowledge rules give insight in the relations between environmental variables and adult pike behaviour, in addition to the results of chapter 7, and may give insight into the habitat suitability of different parts of the river Yser. The rules could eventually allow integrating knowledge from literature and knowledge derived from data into a migration model for pike through the calculation of a HSI in each grid cell.

Only two habitat suitability models for Northern pike were developed in the past. The first was presented by Inskip (1982), who attempted to condense observations in a manageable set of habitat evaluation criteria, structured so as to produce an index between 0.0 and 1.0 of overall habitat quality for Northern pike. He assumed a positive relation between the HSI and carrying capacity of the habitat (U.S. Fish and Wildlife Service 1981). Inskip's (1982) model includes habitat variables believed to be of general importance in limiting the occurrence of pike and is thus exclusively based on expert knowledge. The different levels of an environmental variable are related to an assumed suitability index (SI) and the overall suitability was assumed to be determined by the variable with the lowest suitability index (Figure 8-1). The HSI model accounts for the different life stages of pike and concentrates on the availability of suitable spawning and nursery habitat. The model differs from our HSM, because our HSM is based on data of adult pike and thus does not concentrate on spawning and nursery habitat. The second HSM developed for Northern pike was presented by Mingelbier et al. (2008) and was developed to predict the habitat available for egg deposition

and the early stage mortality by dewatering in the St. Lawrence river. Mingelbier (2008) integrated high resolutional spatial data on flow velocity, wetland type and water temperature in a habitat suitability index, weighted according to literature.

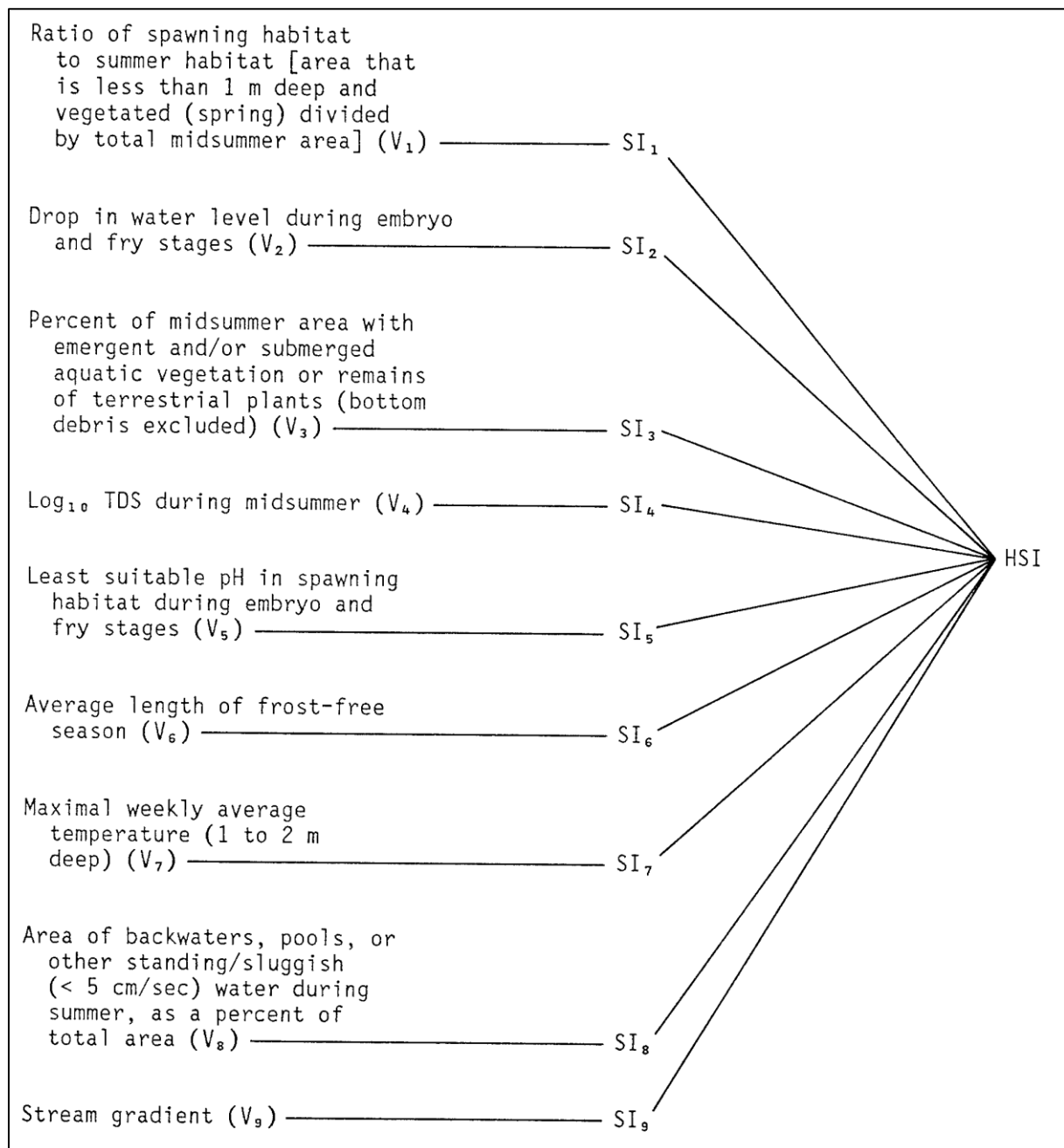


Figure 8-1: Diagram of the HSI model of Inskip (1982) showing the habitat variables included and the aggregation of the corresponding suitability indices (SI's) into a general HSI. The HSI is the lowest of the nine suitability ratings. TDS = Total dissolved solids. The definition of the relations between the variables and the SI's are based on expert knowledge on pike ecology (not shown here).

8.2 Material and methods

The HSM was developed using a rule-based expert model (Liebowitz 1998). In rule-based models knowledge is represented by rules that consist of an IF (antecedent) and THEN (consequent) part as follows (Kampichler et al. 2000):

“IF habitat factor A is high AND habitat factor B is moderate THEN the studied species is absent/its density is low”.

The rule base contains the expert knowledge, which links the input variables with the output variable of the model. The antecedent(s) define(s) when the rule holds and the consequent defines the corresponding conclusion of the rule-based model. The variables that are described in these rules are quantified using linguistic descriptions such as ‘low’, ‘moderate’ or ‘high’ (Kampichler et al. 2000, Mouton 2008). To define the linguistic description for the variable values, membership functions are determined, specifically named sets. If the sets define that a value is either a member to a linguistic value or not, then the sets are called crisp sets and the membership values are limited to 0 (not a member) and 1 (a member; Figure 8-2a). If the sets define that a value may partially be a member of one linguistic value, and partially member of another linguistic value, the sets are called fuzzy sets (Figure 8-2b). The fuzzy set theory was developed by Zadeh (1965) and is particularly useful to process vague expert knowledge and uncertain or imprecise data. Due to their transparency and user friendliness, fuzzy models have been widely applied in environmental modelling (Chen et al. 2010, Liu & Yu 2009, Prato 2009) and more specifically in species distribution modelling (Adriaenssens et al. 2004a, Estrada et al. 2008, Fukuda 2009, Mouton et al. 2011b, Mouton et al. 2009b, Robertson et al. 2004). These models account for the inherent uncertainty of ecological variables and enable expressing non-linear relations between ecological variables in a transparent way (Mouton et al. 2011a). However, the use of fuzzy sets in a rule-based expert model is only interesting if one or more variables are continuous. In the HSM described here, the habitat is described by nominal input variables and the output is defined as a discrete number of pike observations per cell. Hence, there is no need to fuzzify the data and crisp sets were used to derive if-then rules from the habitat and pike data of the river Yser.

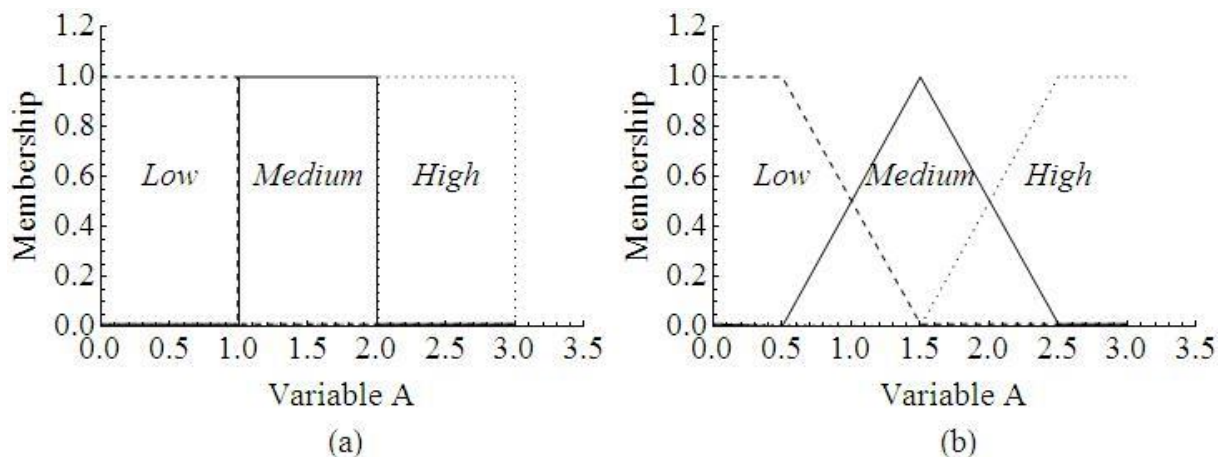


Figure 8-2: Example of the crisp sets (a) and fuzzy sets (b) that are part of the antecedents and consequent of rules in linguistic rule-based models. The membership of the crisp sets ‘low’ (dashed line), ‘moderate’ (full line) and ‘high’ (dotted line) have a sharp upper and lower border, while those of fuzzy sets gradually increase and decrease (adapted from Kampichler et al. 2000).

Sets and rules may be derived from literature knowledge only, or a combination of knowledge from literature and knowledge derived from data. Various techniques have been developed to

identify the rules and sets from data, such as fuzzy clustering, neural learning methods or genetic algorithms (Guillaume 2001, Hüllermeier 2005, Mouton 2008).

The sets of the HSM in this thesis are based on knowledge from literature (A1 publications and grey literature) only. The rules were derived from environmental data and presence/absence data on adult pike collected by radio telemetry in the river Yser (Chapter 3).

8.2.1 Study area and data

We refer to chapter 3 for a detailed description of the study area. The study area was divided in cells of 20 m length and 6 m width and consequently, the area used to develop the model was divided in 6681 cells.

The physical habitat of each cell was assessed by data on the river bank type (the bank type; B, as described in chapter 3), the vegetation type (V, as described in chapter 3), the type of macrohabitat (Ma, as described in chapter 3) and the depth of the macrohabitats (D). Data on the depth were not described at the resolution of the cells, but were used to discriminate between large and small tributaries and side arms. Consequently, the cells of one tributary or side arm had similar depths, being the average, visually assessed depth of the tributary or side arm (Table 3-2). Additionally to the Ma habitat types described in chapter 3, the riparian zone and the open water of the main river were distinguished, since their suitability was expected to differ (Chapman & Mackay 1984a, Kobler et al. 2008b).

The habitat suitability was quantified as the number of pike observations per cell during winter, spring and autumn-summer. The habitat suitability based on B, V, D and Ma was found (chapter 7) and expected to differ between these periods (Chapman & Mackay 1984a, Craig 1996, Jepsen et al. 2001, Koed et al. 2006, Masters et al. 2002, Ovidio & Philippart 2003, Vehanen et al. 2006). As indicated in chapter 3, the periods are defined by the water temperature instead of the date and the pike observations were assessed by radio telemetry.

8.2.2 Model structure

The linguistic values assigned to the environmental variables (the input variables) were defined by crisp sets. The membership functions had rectangular shapes and were defined by four parameters (a, b, c and d): the membership degree goes from zero to one between a and b, from one to one between b and c and from one to zero from c to d (Table 8-1). The parameters of the crisp sets of the input variables were derived from expert knowledge on pike ecology (Casselman & Lewis 1996, Chapman & Mackay 1984b, Craig 1996, De Laak & van Emmerik 2006, Grimm & Klinge 1996, Inskip 1982).

For the definition of the linguistic values assigned to the number of pike observations per cell per season (further named pike density; the output variable) two methods were evaluated (Figure 8-3). In the first method, two crisp sets were used to assign a linguistic value to the pike density: pike absence and pike presence. We further name this method: C2, because two crisp sets were used. Densities of zero were fully considered as pike absence, whereas densities of one and higher were fully considered as pike presence (Table 8-1). In the second method (further named C3), three crisp sets were used to define the linguistic values of low, medium and high pike density to the number of pike observations per cell per season. Pike densities of zero were defined as low, pike densities between one and three were defined as medium and densities higher than three were fully considered as a high density. C3 was evaluated to assess if highly suitable habitats could be differentiated from data noise. The occurrence in the input dataset of zero to three pike observations per cell per season was high in contrast to a high number of pike observations per cell per season (Figure 8-4). The method yielding the most reliable model was selected for further analysis and application.

8.2.3 Model reliability and method selection

The derivation of the rule base that relates the input variables to pike presence or absence from data on the habitat and pike in the study area was performed in the software FISH (Mouton et al. 2012b). Three-fold cross-validation was applied to indicate the robustness of the optimisation results. The folds were created by randomising part of the original data set and assigning each data point to one fold without replacement. To ascertain a prevalence of $\frac{50\%}{50\%}$ for the two output classes (pike presence and absence), the folds were created based on the original data set that contained all cells where pike was observed and as much cells, randomly chosen from the original dataset, where pike was not observed. Generally, a prevalence of 50 % has been suggested to develop reliable models, while extreme prevalence should be avoided (Mouton et al. 2012b).

Models were optimised based on Cohen's kappa (Cohen 1960), which is derived from the confusion matrix (Fielding and Bell 1997; Table 8-2) and ranges from -1 to 1. Cohen's kappa was selected as a performance criterion because model optimisation based on Kappa showed good results in previous studies (Mouton 2008, Mouton et al. 2011a, Mouton et al. 2009a). The confusion matrix indicates the number of correctly and incorrectly classified instances and was calculated here as the average (and standard deviation) of the three folds. The matrix indicates the degree of over- and underprediction of the model. Overprediction or false positive errors occur when the model predicts pike presence in a cell where it was not observed. Underprediction or false negative errors occur when the model predicts pike absence in a cell where it was observed.

To optimise the rule base, a Hill climbing algorithm was applied, specifically the steepest ascent hill-climbing algorithm. The algorithm is described into detail in Mouton et al. (2008). Each iteration the algorithm tests another consequent for a randomly chosen rule, evaluates the performance of the rule base and compares it to the current performance. If the model performs better with the new rule, this rule is selected and another rule is evaluated. Each training iteration is repeated and if the rule base with the highest performance on the test fold is obtained 3 times, training continues on another fold. The final rule base was obtained by selecting the consequents that were minimally 5 times selected as the consequent in all runs of all folds. The performance of the final rule base was calculated as the number of correctly classified instances.

To reduce model complexity, but also computational and monitoring efforts, variables were selected based on the Aikake information criterion AIC (Aikake 1974) or all possible combinations of variables. The latter measure quantifies the balance between model performance and complexity. Although this measure assigns an arbitrary weight to both model characteristics, it provides an indication of how likely a model will generate overfitted predictions. Variables were selected based on the Aikake weight procedure (Burnham & Anderson 2002). These weights quantify the likelihood that a model is the best one, given the data and a set of candidate models. All algorithms in FISH were implemented in a C# toolbox.

Finally, model reliability was evaluated. The most reliable model (1) performs best, which is indicated by the CCI and the confusion matrix, (2) is robust, which is indicated by the similarity in the Cohen's kappa and CCI between three folds, (3) converges best, which is indicated by the similarity in the Cohen's kappa and CCI between several runs within each fold, (4) is applicable on other data than the training data, which is indicated by the similarity in the Cohen's kappa and CCI between training and test datasets and (5) is ecologically relevant, which is (beside the performance and robustness) indicated by the information contained in the resulting rules.

The CCI of the model is calculated as the average of the CCI's of the three folds. The CCI of each fold is calculated as the number of data points in the training and the test dataset that are correctly predicted, divided by the total number of data points.

Table 8-1: Measured variables per 20 m of river length and 6 m of river width, the linguistic values assigned to the input variables of the habitat suitability model (HSM) and the sets describing these linguistic values. Each set is defined by four parameters (a, b, c and d): the membership vertically increases from 0 to 1 between a and b, is equal to 1 between b and c, and vertically or linearly decreases from 1 to 0 between c and d. A triangular membership function is obtained when b equals c and a rectangular (crisp sets) when a equals b and c equals d.

Variable	Class and unit (abbreviation)	Linguistic value	Crisp set parameters
River bank type (B)	Artificial vertical bank (AV)	Low	(0, 0, 1.01, 1.01)
	Artificial foreshore (AF)	Medium	(1.99, 1.99, 2.01, 2.01)
	Semi-natural bank (SNB)	High	(2.99, 2.99, 3.01, 3.01)
Vegetation type (V)	Bare (B)	Low	(0, 0, 1.01, 1.01)
	Reedy (R)	Medium	(1.99, 1.99, 2.01, 2.01)
	Woody (W)	High	(2.99, 2.99, 3.01, 3.01)
Depth (D)	0-0.75 m (VL)	Very low	(0, 0, 1.01, 1.01)
	0.75-1.5 m (L)	Low	(1.99, 1.99, 2.01, 2.01)
	1.5-2.5 m (M)	Medium	(2.99, 2.99, 3.01, 3.01)
	2.5-4 m (H)	High	(3.99, 3.99, 4.01, 4.01)
Macrohabitat (Ma)	Open water of the main river (Op)	Very low	(0, 0, 1.01, 1.01)
	Riparian zone of the main river (Ri)	Low	(1.99, 1.99, 2.01, 2.01)
	Tributary (Tr)	Medium	(2.99, 2.99, 3.01, 3.01)
	Side arm (Sa)	High	(3.99, 3.99, 4.01, 4.01)
Season (S)	Winter (Wi)	Low	(0, 0, 1.01, 1.01)
	Spring (Sp)	Medium	(1.99, 1.99, 2.01, 2.01)
	Autumn-summer (AS)	High	(2.99, 2.99, 3.01, 3.01)
Pike observations	0	Low	(0, 0, 0.99, 0.99)
	≥ 1	High	(2.99, 2.99, 26.01, 26.01) (Figure 8-3a)
Pike observations	0	Low	(0, 0, 0.99, 0.99)
	1-3	Medium	(0.99, 0.99, 3.99, 3.99)
	≥ 3	High	(3.99, 3.99, 26.01, 26.01) (Figure 8-3b)

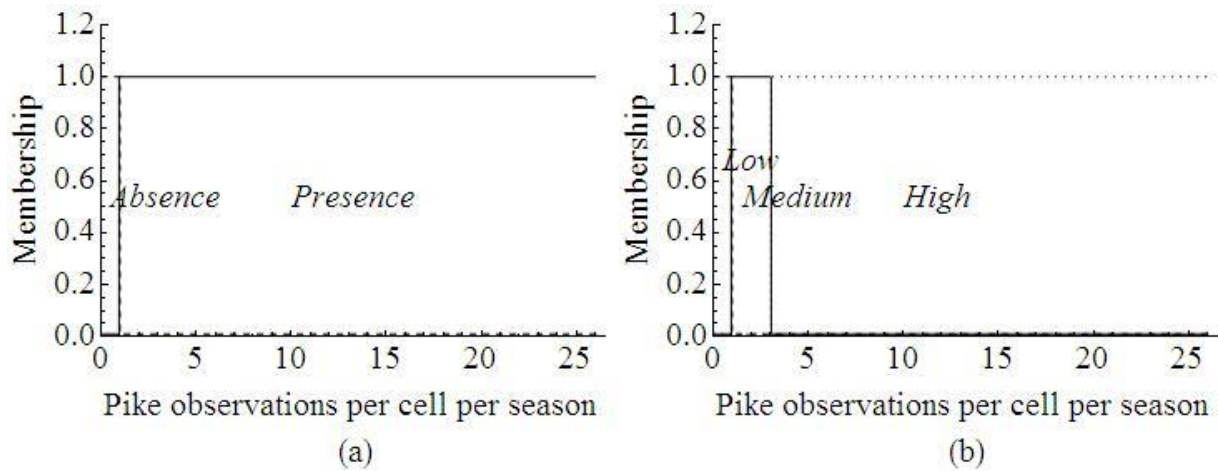


Figure 8-3: Two methods to assign a linguistic value (a: pike absence or presence (model C2); b: low, medium and high pike density (model C3)) to the number of observations per cell per season: by two and three crisp sets (a and b, respectively).

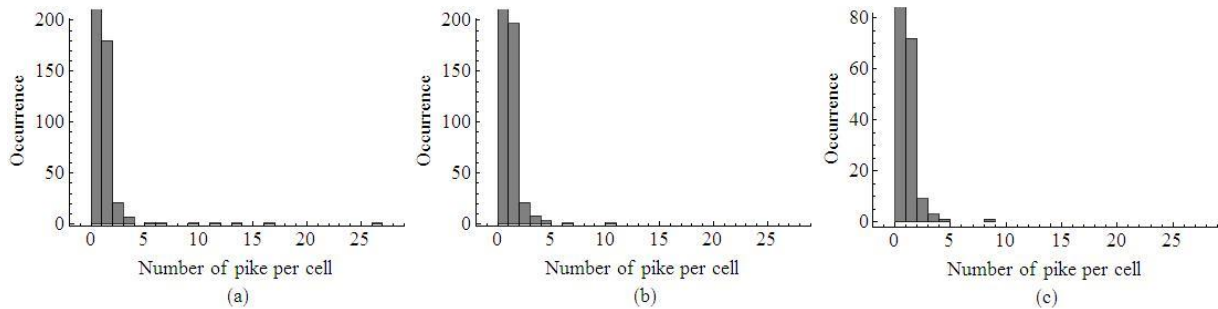


Figure 8-4: The occurrence of the number of pike observations per cell in winter (a), spring (b) and autumn-summer (c). In (c) only occurrences below 80 are shown to better visualise the results. One cell is 20 m length x 6 m width of the river.

Table 8-2: Scheme of a confusion matrix

		Prediction	
		Absence	Presence
Observation	Absence	Correctly predicted absent (named true negative predictions)	Incorrectly predicted present (named false positive errors or overprediction)
	Presence	Incorrectly predicted absent (named false negative errors or underprediction)	Correctly predicted present (named true positive predictions)

8.2.4 Variable selection

To evaluate the relevance of each input variable for habitat suitability prediction, stepwise forward and backward selection was performed. In the stepwise forward selection input variables were added step by step to the model, whereas in the backward selection input variables were removed step by step from the model. In each procedure, five models (since

we investigate five input variables) are developed and evaluated based on the Cohen's kappa of the test dataset. In the stepwise forward selection the highest kappa indicates the best model, whereas in the backward selection the smallest difference between the kappa of the full and reduced model indicates the best model. In the first step of the forward selection the five models contain one input variable each, whereas in the backward selection the models have four different combinations of input variables each. The best performing model is retained and in the next step one variable is added and removed in the forward and backward procedure, respectively. In each model in step 2 another variable is added or removed and the combination of variables is evaluated. The result of the variable selection indicates how much information the input variables and their combination adds to the prediction of the habitat suitability.

8.2.5 Rule base

To define the final rule base that relates the antecedents to the consequent, the robustness and convergence of the model for each rule is evaluated. A rule is robust and fully converged if the prediction of the consequent is similar between all folds and all runs per fold, respectively. These rules are indicated as C+ rules in the remainder of this chapter. If a rule is not robust, but did converge between all runs of each fold, it is indicated as C± rules in this chapter. A rule is not robust and has not converged if either the prediction differs between the runs of one fold (indicated here as C− rules), between the runs of two folds (indicated as C= rules) or between the runs of all folds (C≠ rules).

To define the output class (and thus final rule) in C±, C−, C= rules, the rule coverage and the performance of the folds was evaluated. If the coverage of a C± rule was higher than three, the class of the consequent predicted in seven or eight of nine runs was selected. For C± rules with a coverage of three or lower, C− and C= rules the selection of the output class was based on an evaluation of the performance of the folds. As an additional check, the selected output class of these rules was compared with the output class in the input dataset. No C≠ rules were encountered in this model development.

Since the different habitat types in the study area are homogeneously distributed and since adult pike was expected to be versatile in its habitat use (Chapman & Mackay 1984b), it was not expected that the resulting rules would clearly discriminate suitable from unsuitable habitat types. Therefore, an additional test was performed in which rules are generated that indicate unsuitable habitats by overprediction. The model training of this test was based on the adjusted average deviation (*aAD*). This performance measure includes a parameter α which ranges between 0 and 1 and allows stimulation of overprediction or underprediction. In the test we stimulated overprediction by assigning a value of zero to α . The antecedents of the rules that cause true negative predictions then indicated the potential low quality habitats for adult pike.

8.3 Results

8.3.1 Model reliability and method selection

C2 performed slightly better than C3. The CCI of C2 was 68 %, whereas the CCI of C3 was 64%. For every 718 ± 16 (68 %) instances that are predicted correctly by C2, there were 346 ± 16 (32 %) instances incorrectly predicted, of which 182 ± 16 (17 %) instances were false negative predictions (Table 8-3). In C3 686 ± 79 (64 %) instances were correctly classified in contrast to 379 ± 79 (35 %) instances that were incorrectly predicted, of which 227 ± 79 (21 %) were false negative predictions, as the number of pike observations per cell per season was high or medium but predicted medium and low, or low, respectively. Of the most incorrectly

classified instances in C3 only 2 were predicted low, whereas they were observed high and the largest number of mistakes was made for instances that were observed medium and predicted low (Table 8-5). The balance between under- and overprediction was slightly better for C2 than C3. In C2 15 % of the instances was false positive predicted versus 17 % false negative predicted, whereas this was 21 versus 14 % in C3.

The robustness of C2 and C3 was similar, although the Cohen's kappa and CCI of fold three in C2 were slightly higher than the values in fold one and two, whereas none of the folds in C3 differed much in the values of the performance criteria (Table 8-4, Table 8-6). Relative to the other folds in both models, the difference in Cohen's kappa and CCI between training and test set in fold three of C2 was high, which might indicate that the performance values of this fold are a local optimum. Both C2 and C3 converged well and all performance criteria were similar between the runs within each fold. Only the differences between the values of the training and test datasets differed slightly between the runs and were overall a little higher in C3 (Table 8-4, Table 8-6).

Although the reliability of C2 and C3 was similar, C2 was evaluated slightly better due to its better performance and balance between under- and overprediction. Hence, C2 was selected for further HSM development and application.

Table 8-3: Confusion matrix of the HSM in which linguistic values are assigned to the output variable by two crisp sets (absence: 0 observations and presence: ≥ 1 pike observation).

		Prediction	
		Absence	Presence
Observation	Absence	368 \pm 16	164 \pm 16
	Presence	182 \pm 16	350 \pm 16

Table 8-4: Performance of the converged HSM model defining the output by two crisp sets (presence and absence of pike; Figure 8-3a). Performance was evaluated by the kappa and Correctly Classified Instances (CCI) for a training and a test fold of the input dataset. The best performing run is listed.

Statistic	Performance
Kappa training data	0.38
Kappa test data	0.28
CCI training data (%)	68.87
CCI test data (%)	63.84
CCI full model	67.20

Table 8-5: Confusion matrix of the HSM in which linguistic values are assigned to the output variable by three crisp sets (absence: 0 observations and presence: ≥ 1 pike observation).

		Prediction		
		Low	Medium	High
Observation	Low	384 \pm 50	146 \pm 49	2 \pm 1
	Medium	221 \pm 79	294 \pm 79	4 \pm 1
	High	2 \pm 1	4 \pm 1	8 \pm 1

Table 8-6: Performance of the converged HSM model defining the output by three crisp sets (presence and absence of pike; Figure 8-3a). Performance was evaluated by the kappa and Correctly Classified Instances (CCI) for a training and a test fold of the input dataset. The best performing run is listed.

Statistic	Performance
Kappa training data	0.39
Kappa test data	0.28
CCI training data (%)	68.73
CCI test data (%)	62.99
CCI full model	66.00

8.3.2 Variable selection

The stepwise forward selection indicated that macrohabitat, river bank type and depth added most information to the prediction of the habitat suitability. Macrohabitat type added most information, followed by the river bank type and depth (Figure 8-5). Interestingly, in the first step of the procedure, a model with only vegetation as input variable performed second best. Nonetheless, the addition of vegetation only improved the model in the fourth step of the procedure and did not improve model performance significantly (resulting Cohen's kappa of the unselected models not shown here). Therefore we additionally tested the combination of vegetation with the input variables beside the macrohabitat type. This analysis indicated that vegetation performed best in combination with the macrohabitat type (results not shown here).

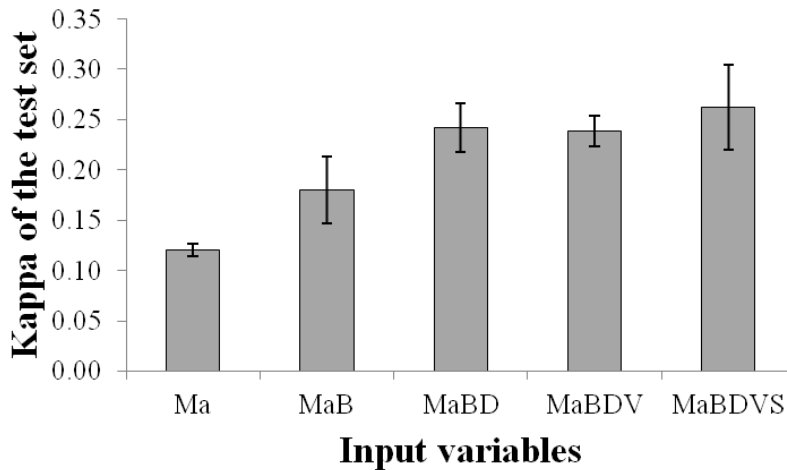


Figure 8-5: Result of the stepwise forward selection, indicated by average and standard deviation of the Cohen's kappa for the test datasets of three runs within three folds. The letters in the x-axis indicate the input variable(s) included in the model (Ma: macrohabitat type, B: river bank type, D: depth, V: vegetation type and S: season).

The stepwise backward selection yielded similar results. The difference between the full and reduced model in the first step of the analysis was smallest for the model without season, followed by a model without vegetation in the next step, then depth and river bank type. The model differing least in performance with the model containing information on river bank type and macrohabitat, was the model with only macrohabitat as input variable (Figure 8-6).

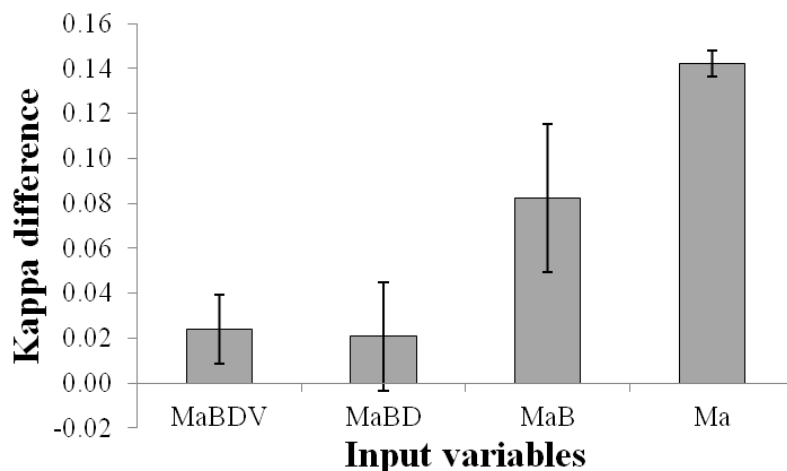


Figure 8-6: Result of the stepwise backward selection, indicated by average and standard deviation of the difference between the full and reduced models in the Cohen's kappa for the test datasets of three runs within three folds. The letters in the x-axis indicate the input variable(s) included in the model (Ma: macrohabitat type, B: river bank type, D: depth, V: vegetation type and S: season).

Since both stepwise selections indicated that addition of vegetation and season did not significantly improve model performance, the CCI and the confusion matrix of a model with only macrohabitat, river bank type and depth (further named the reduced model) was calculated and compared with the confusion matrix of the full model, C2. Although the addition of vegetation and season did not significantly improve model performance, the model with all five input variables performed best. The CCI of the reduced model was 62 % and

specifically 222 ± 1 and 441 ± 1 instances were predicted correctly absent and present, respectively (Table 8-7). Thus, the CCI of the reduced model was lower than the CCI of the full model C2. Although the number of incorrectly classified instances in the reduced model was higher than in the full model, relatively less instances were classified false negative. Specifically, 91 ± 1 (9 %) were classified false negative in the reduced model, whereas this was 17 % in the full model. The number of false positive errors in the reduced model was 310 ± 1 (29 %), which is about three times higher than the number of false negative errors (Table 8-7). Hence, the balance between false negative and false positive predictions was worse in the reduced model than in the full model. The reduced model converged well and all performance criteria were similar between the runs within each fold. Only the differences between the values of the training and test datasets differed slightly between the runs and were overall much smaller in the reduced model than in the full model (Table 8-8). However, since the reduced model overall performed worse than the full model, we selected the latter to define the final rule base of the HSM.

Table 8-7: Confusion matrix of the reduced HSM with macrohabitat, river bank type and depth as input variables, in which linguistic values are assigned to the output variable by two crisp sets (absence = 0 observations and presence ≥ 1 pike observation).

		Prediction	
		Absence	Presence
Observation	Absence	222 ± 1	310 ± 1
	Presence	91 ± 1	441 ± 1

Table 8-8: Performance of the converged, reduced HSM with macrohabitat, river bank type and depth as input variables, defining the output by two crisp sets (presence and absence of pike; Figure 8-3a). Performance was evaluated by the kappa and Correctly Classified Instances (CCI) for a training and a test fold of the input dataset. The best performing run is listed.

Statistic	Performance
Kappa training data	0.26
Kappa test data	0.22
CCI training data (%)	63.10
CCI test data (%)	61.02
CCI full model	62.06

8.3.3 Rule base

Out of 432 potential combinations of the five input variables studied in this HSM, 88 occurred in the dataset on the river Yser and their coverage ranged from 1 to 55. Few rules were covered much and many were covered little (Figure 8-7). There were 59 C+ rules (67 %), 18 C± rules (20 %) and 11 C= rules (13 %).

The evaluation in the input dataset of the consequents of the C_{\pm} and $C_{=}$ rules indicated that four of 18 C_{\pm} rules had a coverage higher than 10 and that they did not converge between all runs of all folds because pike was both observed and not observed in these habitats (Table A.1). The predictions of four of 14 C_{\pm} rules with a coverage lower than 10 was in line with the observations (Table A.1). All $C_{=}$ rules had a low coverage, but the prediction of 10 out of 11 rules was fully supported by the pike observations (Table A.2).

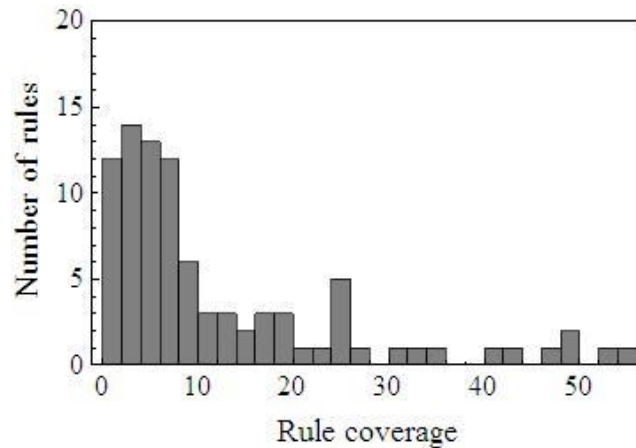


Figure 8-7: Distribution of the coverage of the 88 rules that occurred in the dataset on the river Yser, used to develop the HSM.

In general, the conclusions following from the C_{+} rules did not differ much from the conclusions following from the total rule base and information on the effect of each input variable included in the final rule base was similar to the information included in the C_{+} rules. The rule base confirms that there is no great distinction in habitat types predicting pike presence versus rules predicting pike absence. In winter and spring, adult pike are more likely to occur in the open water, whereas they prefer the riparian zone in autumn-summer (Figure 8-8 and A1 and Table A.3 and A.4). In all periods they are less present in tributaries and in winter and spring they prefer side arms beside the open water. Beside the macrohabitat type, the depth most distinguishes presence rules from absence rules. Most often adult pike use the habitats with >2.5 m depth, but in spring and autumn-summer also shallow habitats of <0.75 m depth are preferred. It is more often predicted absent in habitats between 0.75 and 2.5 m deep (Figure 8-8). Only in autumn-summer slightly more rules including semi-natural banks predict pike presence. Interestingly, in all periods artificial foreshores and woody vegetation predict pike presence more often than pike absence (Figure 8-8 and Table A.4).

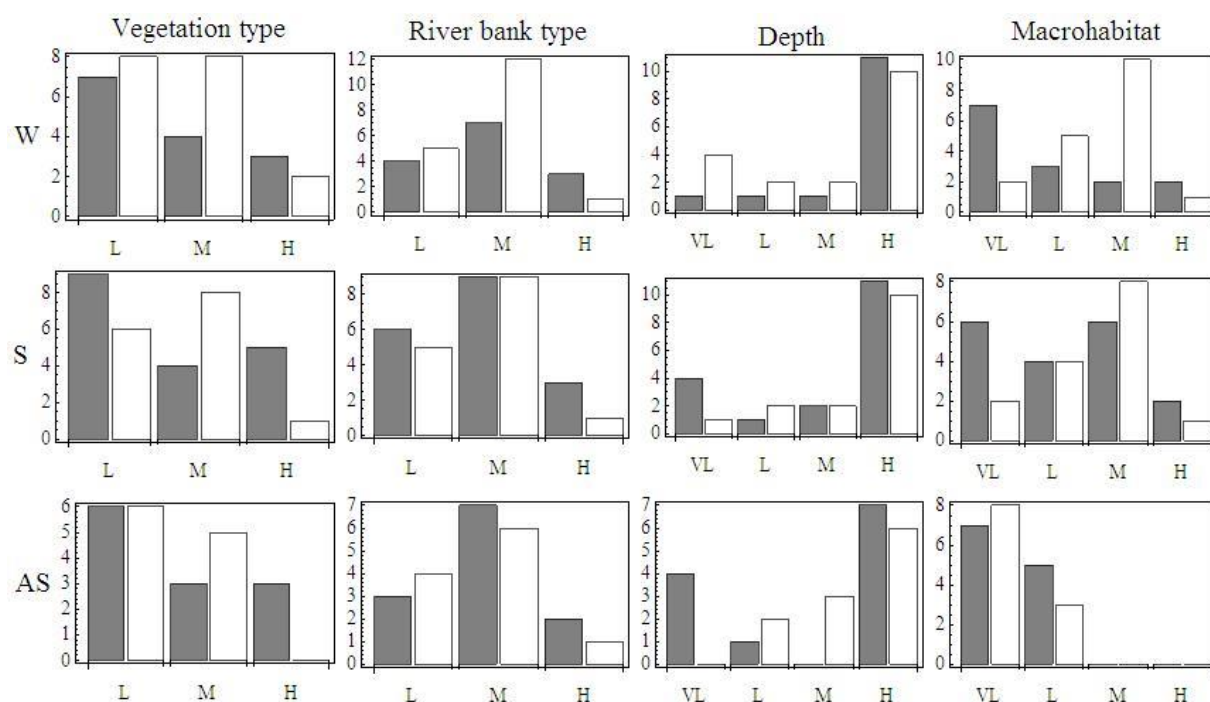


Figure 8-8: Number of occurrences of each variable class in the antecedents of the final rules of model C2 (two crisp sets indicating pike presence or absence) that predict pike presence (grey bars) and pike absence (white bars) for winter (W), spring (S) and autumn-summer (AS).

The rules that correctly predict pike absence in the model that was forced to overpredict mainly indicate absence of pike in the tributaries (Table A.5 and Figure 8-9). The number of rules that contain tributary as macrohabitat type is seven and five in winter and spring, respectively, compared to only one rule for the open water, one rule for side arms and no rules for the riparian zone in both winter and spring. However, this pattern was not found in autumn-summer, when no rule contained tributary and six and two rules contained the open water and the riparian zone as macrohabitat type, respectively (Figure 8-9). Further, pike is relatively most predicted absent for bare banks. In all seasons semi-natural banks were also encountered relatively more in this rule bank than other mesohabitat types (Figure 8-9). These semi-natural banks are mostly related to bare or reedy vegetation (Table A.5). In winter the most shallow and most deep habitats are relatively often related to absence of pike. It is noteworthy that the occurrence of the levels of the input variables is similar for winter and spring and differs for autumn-summer (Table A.5 and Figure 8-9).

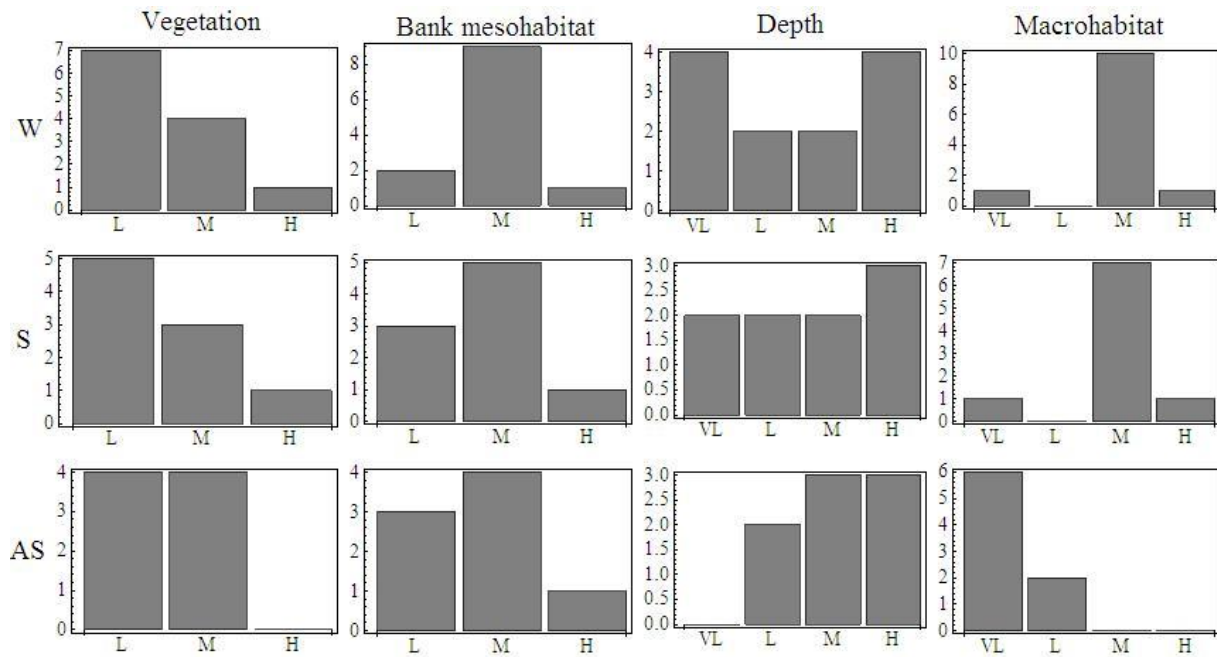


Figure 8-9: Number of occurrences of each variable class in the antecedents of the rules correctly predicting pike absence in model C2 (two crisp sets indicating pike presence or absence) for winter (W), spring (S) and autumn-summer (AS). The model is optimised based on the adjusted average deviation (aAD) and forced to overpredict by assigning a value of zero to α .

8.4 Discussion

8.4.1 Model performance

The model predicting pike presence versus absence instead of low, medium or high number of pike was selected as the most reliable method. Although models C2 and C3 only slightly differed in reliability (mainly due to the slightly better performance and balance between under- and overpredictions), this might indicate that separating medium from high number of pike cell densities has no added value. However, this observation might also follow from the low number of cells having a very high pike density and the high number of cells having a low pike density in this study. If only the few examples of high pike cell densities in the input data set reflect high habitat suitability, then more examples in the input dataset are probably necessary to increase the reliability and performance of C3. Potentially, high pike densities might be missed with radio telemetry, since a limited number of individuals are tracked and high pike densities are only observed if these individuals give up territoriality. However, if a high habitat suitability does not outcompete pike's territorial behaviour, then high habitat suitability is not necessarily reflected in high pike densities and model C2 is truly better than C3 to model adult pike's habitat suitability. Further research on the relation between habitat suitability and the presence of other pike, beside an analysis on radio telemetry versus fish catches as sampling method, might clarify this.

The overall performance and reliability of C2 is not substantial. Generally accepted minimal values for CCI and kappa indicating good model performance are 75% and 0.4, respectively. In the HSM developed here on average one prediction is false on every three predictions that are made (CCI = 68%). Half of these false predictions (15 of 32%) are overpredictions and are thus not necessarily false, but half are underpredictions and are thus true model errors. Overprediction may be due to unbalanced colonisation of habitats (Mouton et al. 2012b), which may follow from the occurrence of migration barriers, temporal population variations

or sampling inefficiency (Barry & Elith 2006, MacKenzie et al. 2003, Mouton et al. 2012b). No migration barriers occur in the study area and the large home ranges of the studied pike (see chapter 3) do not suggest that the animals are forced in a part of the study area. Furthermore, the results of this chapter and chapters 6 and 7 do not indicate high temporal variation in behaviour. Consequently, the overpredictions might follow directly from sampling inefficiency, which could be attributed in this study to the number of studied fish, which might have been too low or the study area, which might have been too large to capture pike presence at all locations that actually have suitable habitat for adult pike by radio telemetry. Nonetheless, following a larger number of fish in this study area is practically not possible (see also the discussion chapter 6 and 7). Whether electro- and fyke fishing would have yield a more optimal model is not sure, since these methods are not very efficient to capture adult pike. In a previous study on modelling the habitat suitability of burbot (*Lota lota* L.) the two sampling methods (telemetry versus electro fishing) were compared and radio telemetry yielded a better performing model (Mouton et al. 2012b).

Since the performance of the HSM presented here was not substantially large, other modelling techniques such as classification trees, random forests and support vector machines were briefly evaluated by application on this dataset (results not shown here). However, none of the tested modelling techniques better performed than the rule based method described in this chapter. Other methods that could be evaluated in the future to further enhance model performance and reliability are:

- Use of all data instead of $\frac{50\%}{50\%}$ prevalence and weighing of the absences according to their relative occurrence in the full dataset;
- Restrict the input dataset to the data within each pike's home range;
- Include other input variables beside the five variables investigated here.

8.4.2 Variable selection

The selection of macrohabitat type indicates that this variable discriminates most between the presence and absence of adult pike in this study. Beside depth, this variable contains information on the habitat at the macro-scale. A further improvement of the model performance followed from additional information on the river bank type and the depth. Although vegetation was the second most important variable in the first analysis of the forward selection, it only added information (and not significantly) after addition of mesohabitat type and depth. Generally, these results might indicate that adult pike chose the habitat only at a broader scale (macro-scale), but are versatile in their habitat use at a smaller scale, specifically when it comes down to the vegetation type. To evaluate whether preference for vegetation type was present at a broader spatial scale than the meso-scale (20 m), we applied the analysis presented by Crook et al. (2001) on the scale dependence of adult pike's vegetation type preference. This analysis indicated no significant preference at other scales than the one investigated here (results not shown here). A future analysis according to Crook et al. (2001) on the scale dependence of other habitat variables might further underpin the hypothesis that adult pike select the habitat at a broader scale based on macrohabitat characteristics.

Notwithstanding the non-significant improvement of model performance following the addition of vegetation and season, a model with all five variables performed slightly better, which might suggest the presence of important relations between vegetation and season and the other input variables. However, it would be interesting to additionally evaluate the rules following a model with three variables in the future, since model complexity is then reduced.

8.4.3 Rule base

Twenty percent (89 rules) of all possible rules (432 rules) occurred in the dataset of the river Yser. Few of these rules were covered much and many were covered little. The majority of the rules in the final rule base were robust (87%), of which again the majority converged between all runs of all folds and were thus reliable. The output of the rules that were not robust and did not converge was still very much in line with the input dataset, overall indicating robustness of the final rule base.

The ecological information resulting from the final rule base was very much in line with the results of the direct analysis of adult pike habitat use and preference in this thesis (chapter 7). As expected based on the high individual difference observed in chapter 7, beside previous observations on the versatile habitat use of adult pike (Chapman & Mackay 1984b), no clear differences in rules predicting pike presence versus rules predicting pike absence was observed. For instance rules containing semi-natural banks, artificial vertical banks or bare vegetation almost evenly often led to prediction of presence than prediction of absence. Rules that did more or less discriminate between presence and absence of pike and thus habitat suitability were related to the macrohabitat type and depth. These variables were the most and third most important variables, respectively, in the variable selection analysis. Rules containing tributaries as the macrohabitat type relatively often predicted pike absence, specifically in winter. This was also confirmed by the occurrence of tributaries in the rules correctly predicting pike absence, which suggests a relative low habitat suitability of tributaries for adult pike. Only in spring in combination with the most shallow macrohabitats, tributaries were predicted suitable. This is in line with the results of chapter 7 and underpins the knowledge on pike ecology during spring (the spawning season in this region; De Laak & van Emmerik 2006, Grimm & Klinge 1996, Inskip 1982). Further, a relative high habitat suitability is suggested for side arms, as side arms were not often encountered in the rules correctly predicting pike absence and relatively more present in the rules predicting pike presence in the final rule base of C2, specifically in winter and spring. However, in winter and spring relatively most predictions of pike presence were related to the open water. Generally, pike was most often predicted present in the most deep and most shallow habitats, but these habitats were also relatively most present in the rules correctly predicting pike absence. It is indicated that the habitat types that were most present in the study area least discriminated between presence and absence of adult pike. In line with this, the relative high suitability of woody banks and artificial foreshores appeared from the final rule base and the rules correctly predicting pike absence. This observation is in line with the high preference for these habitat types by some of the studied animals.

Generally, no substantial differences between winter and spring were observed. The differences observed between autumn-summer and the other two seasons are in line with knowledge on pike ecology (Craig 1996, Inskip 1982, Kobler et al. 2008b). However, they might also follow from the relatively lower number of observations for this season.

In the first place, the HSM was developed to integrate data and knowledge on the relation between adult pike and the river bank type, bank vegetation, depth and flow conditions and to integrate it in an adult pike migration model. Although the development process and resulting rule base provide useful information on adult pike habitat suitability in the river Yser, the HSM should be optimized further to use it for reliable predictions of adult pike distribution in the river Yser.

CHAPTER 9

General conclusions and further research

9.1 General conclusions

This section gives an overview of the main conclusions of the research concerning the spatially explicit modelling of pike migration in support of river management using the IBM and CA modelling techniques, and generally discusses them. We focus on the conclusions on the evaluation of the CA and IBM based modelling techniques for the simulation of pike migration. Besides, we conclude on the information on pike ecology and its relevance for management arising directly from the field study and indirectly from the habitat suitability model.

9.1.1 CA-based model versus IBM to simulate pike migration

The success of management plans to restore river habitats and enhance the accessibility requires an efficient allocation of the efforts beside an assessment of the impact of each measure on river ecology. Therefore, good knowledge on the status of the aquatic system, the main bottlenecks and the ecology of the target species is essential. Integrating this knowledge in models can help to quantitatively predict the impact of a specific measure and may help to better understand the habitat requirements and spatial dynamics of the fish. Habitat suitability and species distribution models are helpful tools in understanding the suitability of local, critical habitat variables such as water depth, flow velocity and vegetation characteristics and have thoroughly been studied during past decades. However, these models do not allow to model population viability constraints by wider, large scale variables, such as migratory access. In chapter 1 we indicated the possible consequences of this for the support in river management decisions on for instance solving migration barriers and the rehabilitation of river banks. Hence, indicating the benefit of modelling spatially and temporally.

Two eligible modelling techniques that may account for these factors are IBMs and CAs. Consequently, the aim was to evaluate the applicability of these modelling techniques for the simulation of pike migration. Our review on the use of these modelling techniques in modelling fish migration indicated that IBMs have already been applied multiple times to

simulate fish migration, whereas the application of CAs for fish migration modelling is very limited. None of the techniques was ever applied on Northern pike before. Past research furthermore indicated that IBMs and CAs are both able to simulate very complex systems, but that IBMs usually require much parameters and numerical simulations for this, which makes them very complex to understand and communicate, whereas CAs are very transparent and still enable modelling of very complex systems.

The evaluations performed in this thesis support these findings, but indicated that it is very difficult and perhaps more difficult than assumed, to link spatial and temporal processes in a CA and to find the transition rules that enable the simulation of a complex system, such as pike migration.

The evaluation of the IBM in chapter 5 indicated that pike movement and migration can be simulated in a detailed level, for instance by accounting for differences in the effect of the environment on movement and migration according to time, by accounting for temporally varying home ranges and by accounting for territoriality per individual pike. A major advantage of the IBM towards river management, arising from the evaluation in chapter 5, is the ability to tune the parameters so that the model gets applicable on other fish species or other study areas. Furthermore, further fine tuning of the parameters based on more field data or new knowledge is possible and can further enhance the accuracy of the model for pike. As indicated in the discussion of chapter 5, such new knowledge could be related to the territorial behaviour of pike. Due to the ability to account for detailed information on pike's ecology and behaviour, the model was already quite accurate even though it was still only generic and needs further fine tuning. The fact that individuals were modelled allowed validating the model with radio telemetry data.

In contrast, the evaluation of the CA based model in chapter 4 indicated that the CA was sensitive to the grid resolution, the number of pike in the grid and the initial distribution of the pike over the grid. Even after adaptation of the neighbourhood, which was expected to enable the coupling of time versus movement, and inclusion of a carrying capacity per grid cell, the model was still sensitive to low pike densities. Hence, the results indicated the difficulties in coupling the different physical and ecological scales of an ecosystem spatially and temporally and finding the correct transition rules that deal with this. Following this sensitivity, the model was not further updated with new information on pike habitat use and migration following from the analyses on the field data collected by radio telemetry described in chapters 6, 7 and 8 and neither validated.

The results of the model evaluations and the large individual variance observed in the adult pike telemetry data are in favour of the IBM technique for simulation of pike migration and potential future coupling with a population growth model. However, we also suggest that further research on the transition rules of the CA-based model might result in a CA that is not sensitive to the model settings and able to simulate pike migration in a transparent way.

9.1.2 Adult pike ecology and management

As indicated in chapter 1, the status of pike in Flanders has declined substantially in the previous century due to water quality and habitat deterioration and obstruction. Loss of natural river habitats by embankments, canalizations and artificial water level management is in general a threat to the fish fauna. Often spawning and rearing areas for juveniles are most affected and pose the biggest bottleneck in the successful survival of the population. In the present study, however, only adult pike are studied and the study specifically focused on the relations between water temperature and flow on adult pike migration, and macro- and mesohabitat characteristics and adult pike behaviour. Large pike are subjected to low predation risk, and from this and previous studies we know they may use both littoral and pelagic areas and this may be irrespective of vegetation and other covers, i.e. they are not year

round bound to the riparian zone. Further, their habitat use is most probably connected to foraging activity, and they will seek to areas which may give high foraging success, i.e. to areas with high density of prey fish. Accordingly, the habitat use of large pike is not the best indicator for a more efficient management of pike rivers. Nevertheless, the movement and migration dynamics and the habitat use of large pike is part of the life cycle of the species, and as such of importance.

The analysis on the relation between environmental variables and migration revealed that four environmental variables significantly affected pike migration, ranging from the location where pike were observed (strongest effect), over water temperature and flow to the diel water temperature change (weakest effect). The results on the relation between water temperature and migration in our study suggested that 9 to 10 °C might be a threshold level for migration in this region, since the activity was highest at ca. 9 °C and there was only a one-day time lag between migration peaks and temperature peaks exceeding 10 °C. The decrease of the movement rate at temperatures above 10 °C, indicated that pike had arrived at their spawning area by then. The results on the relation with flow showed an inhibition of the migration rate at high flows.

Based on our results river managers could consider the impact of water temperature on pike migration to facilitate the accessibility of small tributaries and spawning grounds, e.g. by opening valves at water temperatures between 0 and 12 °C. The apparent inhibition of pike migration at high flows suggests that pike could benefit from the buffering of peak flows, e.g. by restoring floodplains and increasing lateral connectivity. Further integration of these results in the IBM on pike migration could improve the IBM and help to better understand and simulate the effect of for instance check valves at the outlet of tributaries as illustrated in chapter 1.

It is notable how the previous studies on pike movement and migration dynamics, often investigated in relation to environmental variables and habitat use, differ in their conclusions. The dissimilarity was also observed in studies on pike's diurnal activity, on the grouping of pike into sedentary and active animals and on the pike length-movement rate relation. These differences might not only reflect variation in pike behaviour among different ecosystems, but also differences in method and study design. In this respect, the most important differences between our study and the aforementioned pike telemetry studies are the shape (lake versus river) and the length of the study area, beside the statistical method applied compared to the migration studies.

Our study on the habitat use and preference of adult pike revealed that the dissimilarity in studies might also follow from large individual differences in the behaviour of adult pike. Both at the macro-scale and the meso-scale pike individually differed significantly in habitat use, and habitat preference at the meso-scale. Our results suggest that these individual differences might be of greater importance for pike management than previously thought. Specifically, if research could further underpin that individual adult pike have a very dissimilar habitat preference, then this might strongly support the need to protect the level of habitat diversity in a river system.

The habitat diversity can be protected or enhanced at different levels. First, river managers could focus on the heterogeneous distribution of existing suitable habitats in the river system. As also illustrated in scenario 4 of Figure 1-1, a pike population might benefit more from small parts of suitable bank habitat that are spatially separated than from one long suitable bank which is located too far to reach it. If such habitats are present in the area but not connected then the population might strongly benefit from improving this lateral connectivity. This was indicated in this study by the intense use by several pike of side arms and tributaries beside the main river. If such habitats are not present and then parts of large unsuitable habitat might be rehabilitated by for instance fore shores or artificial side arms. Our study indicated

that the effectiveness of such rehabilitated habitats might be lower than was expected. During this study, none of the tagged pike were observed to use the artificial side arms in the river Yser. We did not evaluate the potential reason underlying this observations, but this should definitely be further investigated to improve the suitability for adult pike of these artificial habitats.

The suggested importance of habitat diversity was also supported by our observations on the habitat use and preference of adult pike on the meso-scale. Irrespective of assumptions on the habitat availability and use, semi-natural riparian habitats were always relatively most used. In contrast to the semi-natural banks, artificial foreshores were never significantly used. The results of habitat use were compared to a selection ratio of habitat preference and this revealed that although pike significantly used semi-natural banks, they only significantly preferred it in winter and in combination with reedy vegetation. Further, the habitat preference analysis revealed large individual differences, but no substantial preference for the riparian habitat at the population level.

Lastly, the observations from the telemetry study on the location of juvenile pike in the area around the river Yser suggest the importance of a potentially small number of tributaries. Although more of these assumed-suitable tributaries are present in the study area, no juvenile pike were observed there. It appears that the tributaries visited by tagged adult pike and containing juvenile pike are the only of very few suitable tributaries in the area of the river Yser, this has important consequences for the pike/river management in the basin of the river Yser. In that case, these tributaries and their surrounding area should be even more protected from water pollution and habitat degradation. It could further be investigated if other mechanisms, such as homing behaviour or specific individual preferences underlie the choice of these specific habitats, specifically spawning habitats by adult pike or not.

9.1.3 Analysing pike movement data and habitat use

To collect data on adult pike behaviour in a river and subsequently analyse these data to gain information on the habitat requirements and potential limitations of the animal, different techniques are available, of which the telemetry techniques were described in chapter 3. The difference in these techniques follows from the tag type and signal used to transfer information on the location and environment of the tagged animal. Out of all available techniques radio telemetry allows to exactly position an animal to a few meters precise. Radio telemetry requires to approach the tag and to seek the correct frequency with a receiver. Consequently, this is a time consuming activity and therefore more appropriate for studies over a relative short period or a relatively small study area and with the purpose to exactly evaluate the habitat use. We applied the technique here, because at the time of the study budget and experience was lacking to apply a potential one other suitable technique allowing precise positioning, acoustic telemetry.

Our study area entailed > 60 km of accessible river channels and pike were tracked for one year. Following the size of the study area, we could maximally tag 15 adult pike that were located every day to every two days in winter and spring, and every week in autumn and summer. This sometimes yielded sampling intervals of a few days if an animal could not be tracked during one tracking event. The study of Baktoft et al. (2012) indicated that long sampling intervals may entail a great sampling error. This is also applicable on our study, even though this sampling error was minimized by only lowering the tracking frequency when reduced activity was observed. Hence, it was necessary to evaluate this error. We evaluated this error by calculating the TTI and the dependence of the observations collected during 24 h sampling campaigns. The results of the analysis revealed that if the adult pike would have been tracked every 2.5 hours, not much information on their diel habitat use would have been missed. Further, every 20 to 24 hours the locations were dependent, which suggests the

existence of a dial cycle in the movement patterns of the fish. This result further means that variation in the timing of the localisation of every individual throughout the regular trackings, is important to get correct insights into the pikes' habitat use and preference. To get better insight in the amount of sampling error following from the regular tracking protocol, the TTI and dependence analysis proposed by Swihart and Slade (1985) should be adapted so that it is also applicable on data locations in a meandering river. For now, this is not the case and further research is thus desirable in this respect.

9.2 Indications for further research

The analysis and results presented in this thesis provide valuable insights that could be used in the further development of models that enable the prediction of the effect of river rehabilitation options on adult pike or other adult fish species. This development requires a further integration of the results following from direct studies on fish migratory behaviour and habitat use, evaluated by the correct available methods, and none sensitive modelling methods. Here we indicate what further steps may be taken to enhance the study on both aspects (modelling and ecology) before any integration is performed. For now, the new insights and information on pike ecology following the analysis of the telemetry data was not integrated yet in the developed models. The reason for this is that the models were developed as an evaluation of their applicability for simulating pike migration in the first place. Besides, the evaluation indicated sensitivity to model settings of the CA-based model and thus the modelling method should be enhanced prior to further knowledge and data integration.

9.2.1 CA-based model versus IBM to simulate pike migration

We suggest the following aspects of the IBM could further be developed and investigated to enhance the simulation of pike migration. First some of the model parameters could further be fine-tuned based on information arising from the analysis of the radio telemetry data in this thesis. Specifically, these are the dimensions of the pike home ranges and the movement speed per season, beside the shape of the trapezoidal sets that define the timing of the migration behaviour. The latter could be related to water temperature instead of the date according to the results of chapter 6. Other model aspects that could be optimised are the definition of the initial pike distribution and the allocation of a potentially new home range after spawning. Further, after validation of these adaptations, it could be considered to add a growth module to the model.

Following the results of chapter 4, we suggest a solution should be looked after to deal with the model sensitivity to the grid resolution and low pike densities in the grid. Currently, it is not possible to simulate pike migration when the density is one pike per grid cell, even not after adaptations of the HSI and neighbourhood definition. This suggests that a potential solution lies in the adaptation of the transition rules. Therefore we suggest further research clarifies how the transition rules could be adapted so that the simulation of low pike densities is enabled. We hypothesize that this further increases the number of optimal trade-offs between pike density and grid resolution for which the model correctly simulates. Further research is necessary to evaluate this before any further knowledge or data are integrated and the model is validated.

9.2.2 Adult pike ecology and management

The lack of complete certainty on the occurrence of spawning after migration was encountered as a limitation here to exclusively investigate the triggers for spawning migration. To overcome this problem, future research on the triggers of migration could be expanded by an identification of the true purpose of each migration. For instance, accelerated

failure time or Cox regression (Castro-Santos & Haro 2003) could be applied to analyse the triggers for spawning migration. Besides, it could reveal how many individuals of the population spawn and migrate to spawn, and how many spawning migrations occur per individual during one spawning period. This information may be very important to further reveal bottlenecks in the sustainability of a population and directly support river managers with information on potential important migration barriers and the location of suitable spawning habitat.

Some important new research questions on the migration dynamics and habitat use of adult pike that have been uncovered during this research are:

- Why are the artificial river side arms in the river Yser not suitable or attractive for adult pike?
- Does pike spawn in other tributaries than those observed in this study?
- Why would pike spawning areas be so restricted and what are the key variables defining the suitability of these spawning habitats.
- Are there other mechanisms, such as homing, beside certain specific habitat requirements that determine the choice of the spawning location by adult pike?
- How many pike do actually spawn?
- How territorial is pike?
- What key variables determined the high use of the side arms by several individuals in winter?
- What is the effect of depth on pike habitat use and preference?
- What is the extent of the variation encountered between the individual pike and how representative were the twelve studied pike from this study?
- How much information on pike movement and migration dynamics is missed in a sampling protocol of three samplings per week or less?

We suggest the second question can be answered by more and repeated measures and a multivariate analysis of the data linking environmental variables such as water quality variables and juvenile pike presence or absence. To answer the question on how many pike actually spawned could be answered by sampling more individuals and calculating a Cox regression as indicated earlier. To clarify the extent of the individual variation simply more individuals need to be investigated. Finally, the last question could be investigated by the combined use of telemetry tags and accelerometers that indicate for instance the tail beat frequency of the fish.

Next, we suggest that the results and insights resulting from the analyses described in chapters 3, 6 and 7 and the HSM development described in chapter 8 might be extended by addition of a more detailed description of the depth used by pike. In the analysis of habitat use and preference, depth data were not taken into account and in the HSM depth was only considered at the macro-scale. However, the results of the variable selection in chapter 8 and previous research on pike ecology indicates the potential importance of depth in the behaviour of adult pike. Although this is practically nearly impossible to account for, it would furthermore be interesting to integrate information on the distribution of pike's prey. Potentially much of the behaviour of large, adult pike could be explained by pike following their prey and potentially it may declare part of the large individual differences found in this and previous research. This hypothesis has been suggested previously by Masters et al. (2002) but was not investigated in any study of adult pike habitat use and preference so far. Another research topic that we suggest could be further analysed with the data collected during this thesis is the relation between flow and water temperature and the use of the riparian zone versus open water.

To further enhance the prediction of pike presence and absence based on pike data and ecological literature knowledge we suggest the following aspects of improvement on the

developed HSM. First, it would be interesting to compare the presented rule base following from the full model, with the rule base following from the reduced model. The small difference in performance between the two models may not outweigh the added complexity of considering five instead of three variables, and this should further be investigated. Furthermore, since season seemed not an important variable and since the number of pike locations differed between winter and spring, and autumn-summer it might be better to omit this variable from the model. Further, as previously indicated, the depth data could be added in a higher resolution and consequently the crisp sets for this variable could be fuzzified. Similarly, it would be interesting to further assess the effect of fuzzifying the output class for one to three pike observations per cell. One final aspect that we consider a shortcoming in the development of the HSM in this thesis is the methodology applied to select the output class of the rules that were least robust and did not converge. More simulations could have been applied to select the correct output class per rule. However, although this would further improve the ecological relevance of the model, the resulting small differences between the information contained in the robust, converged rules and the complete rule bank, do not suggest large differences in the final conclusions of the model following the suggested improvement.

9.2.3 Analysing pike movement data and habitat use

In chapters 6 and 7 we presented a statistically underpinned approach to analyse the complex non-linear relation between environmental variables and fish migration. Besides, we described and applied a method to evaluate the habitat use and preference that allows accounting for different assumptions on the habitat availability and use. For the latter analysis pike's home ranges were determined based on the BBK method. We suggest that the applicability of this method for the correct determination of the home ranges could further be investigated and specifically, could be compared to previous methods presented in literature on home range calculations. We selected the BBK method in this thesis because this is the only method accounting for a temporal component. Hence it is the only method accounting for potential problems arising from the dimensions of the study area (which is a meandering river and thus very long and not wide compared to most territorial study areas).

A final indication for further research regarding the analysis of the radio telemetry data is the applicability of the TTI analysis on the telemetry data of the regular trackings. The method presented in this thesis was not applicable on pike observations that are distributed upstream and downstream of a meander. However, this is necessary to get insight into the amount of error arising from the tracking protocol at a wider time frame. As already indicated above applying a Cox regression on the telemetry data to analyse the occurrence of a certain event, such as the blocking of fish migration by a check valve could further be applied on these or other pike data and the use of accelerometers in combination with positional tags might indicate important new information on the timing and location of spawning.

9.3 Contributions of this thesis

The aim of this thesis was to provide insight into the applicability of the IBM and CA modelling paradigms for simulation of adult pike migration, the movement and migration dynamics, and the habitat use and preference of adult pike in a lowland river and the methodology to properly evaluate the habitat use and preference of migratory fish. Therefore, different methodologies were applied and evaluated and pike data were collected and analysed. As the models were evaluated and one of the models was found to be sensitive to model settings, the models were not updated further with new knowledge and data on pike ecology following from the telemetry study. However, the potential advances and

shortcomings of doing have been clarified now. As such, this thesis contributed to both the spatially explicit simulation of pike migration, knowledge on pike ecology with direct suggestions for river management and the methodology on properly analysing telemetry data from riverine fish. These contributions are the following:

- the strengths and weaknesses of two eligible techniques to spatially explicit simulate migration were illustrated;
- an IBM on pike behaviour in a river was presented that could be further applied on adult pike after fine tuning of the parameters based on knowledge and data;
- a method to analyse the complex non-linear relations between pike migration and continuous environmental variables was presented and applied;
- a method to analyse the habitat use and preferences for a riverine fish, while accounting for assumptions on habitat use and availability was presented and applied;
- a method to assess the loss of information following the applied radio-tracking protocol was presented and applied;
- insight into the migration dynamics, habitat use and preference of adult pike over several seasons in a lowland river was provided and suggestions for river management were described, beside new uncovered research questions that could be investigated to better understand the behaviour and ecology of adult pike;
- a data-driven rule base on the habitat preferences of adult pike in a lowland river was developed.

Appendix A: Details on the final rule base of the HSM described in chapter 8

Table A.1: C_{\pm} rules (similar consequent in all three runs of all folds but different consequent in one fold of a three-fold cross-validation) resulting from C2 (two crisp sets indicating pike presence or absence), linking the antecedents (see Table 8-1; vegetation: bare (B), reedy (R) and woody (W); river bank type: vertically reinforced (AV), semi-natural (SNB) and artificial foreshore (AF); depth: very low (VL), low (L), medium (M) and high (H) and macrohabitat type: open water (Op), riparian zone (Ri), tributary (Tr) and side arm (Sa)) to pike presence and absence per season (winter (Wi), spring (Sp) and autumn-summer (AS)) and indication of the occurrence of the number of pike observations in the dataset used to develop the model. Bold text indicates the rules for which the observations best support the outcome of the converged folds.

Rule	Season	Rule coverage	Occurrence of the number of pike observations in the input dataset			
			10	2	1	0
Pike predicted present						
B:R:H:Ri	Sp	49	0	2	23	24
B:AF:H:Op	Wi, Sp	3, 4	0	0	2, 2	1, 2
W:AV:H:Tr	Sp	1	0	0	1	0
W:AV:H:Op	Wi, AS	3, 1	0, 0	0, 0	2, 1	1, 0
R:AF:H:Op	Wi	6	0	0	4	2
W:SNB:H:Op	AS	5	0	0	3	2
B:AV:VL:Tr	Sp	2	1	0	0	1
W:AV:H:Ri	Sp	4	0	0	2	2
Pike predicted absent						
B:AV:H:Ri	Sp	48	0	1	21	26
B:SNB:H:Ri	Wi	47	0	1	18	28
R:AF:H:Ri	Wi	9	0	1	3	5
R:SNB:H:Tr	Sp	7	0	0	3	4
W:AV:H:Ri	Wi	5	0	0	2	3
W:SNB:H:Tr	Sp	5	0	0	1	4

B:SNB:H:Op	AS	16	0	0	7	9
B:AF:H:Ri	Sp	6	0	0	2	4

Table A.2: C= rules (similar consequent in all three runs of two folds of a three-fold cross-validation) resulting from C2 (two crisp sets indicating pike presence or absence), linking the antecedents (see Table 8-1; vegetation: bare (B), reedy (R) and woody (W); river bank type: vertically reinforced (AV), semi-natural (SNB) and artificial foreshore (AF); depth: very low (VL), low (L), medium (M) and high (H) and macrohabitat type: open water (Op), riparian zone (Ri), tributary (Tr) and side arm (Sa)) to pike presence and absence per season (winter (Wi), spring (Sp) and autumn-summer (AS)) and indication of the occurrence of the number of pike observations in the dataset used to develop the model. Bold text indicates the rules for which the observations best support the outcome of the converged folds.

Rule	Season	Rule coverage	Occurrence of the number of pike observations in the input dataset			
			10	2	1	0
Pike predicted present						
R:SNB:M:Tr	Sp	3	0	1	1	1
B:SNB:L:Ri	AS	2	0	0	2	0
R:AF:H:Ri	AS	2	0	0	2	0
R:AF:H:Op	AS	1	0	0	1	0
B:SNB:VL:Ri	AS	1	0	0	1	0
Pike predicted absent						
R:SNB:M:Tr	Wi	3	0	0	0	3
B:SNB:L:Op	AS	2	0	0	0	2
B:AV:VL:Tr	Wi	1	0	0	0	1
R:SNB:L:Op	AS	1	0	0	0	1
R:SNB:M:Op	AS	1	0	0	0	1
B:AF:H:Ri	AS	1	0	0	0	1

Table A.3: C+ rules (similar consequent in all nine runs of a three-fold cross-validation) resulting from C2 (two crisp sets indicating pike presence or absence), linking the antecedents (see Table 8-1; vegetation: bare (B), reedy (R) and woody (W); river bank type: vertically reinforced (AV), semi-natural (SNB) and artificial foreshore (AF); depth: very low (VL), low (L), medium (M) and high (H) and macrohabitat type: open water (Op), riparian zone (Ri), tributary (Tr) and side arm (Sa)) to pike presence and absence per season (winter (Wi), spring (Sp) and autumn-summer (AS)).

Pike presence			Pike absence		
Rule	Season	Rule coverage	Rule	Season	Rule coverage
W:SNB:H:Ri	Wi, Sp, AS	11, 11, 6	R:AV:H:Ri	Wi, Sp, AS	25, 33, 6
B:AV:H:Op	Wi, Sp, AS	30, 25, 12	R:SNB:H:Op	Wi, Sp, AS	55, 41, 27
B:SNB:VL:Sa	Wi, Sp	5, 20	R:AV:H:Op	Sp, AS	12, 4
B:SNB:L:Sa	Wi, Sp	7, 7	B:AV:H:Ri	Wi, Sp	43, 48
W:SNB:H:Op	Wi, Sp	12, 9	R:SNB:L:Tr	Wi, Sp	3, 4
B:AV:M:Tr	Wi, Sp	15, 19	B:SNB:L:Tr	Wi, Sp	7, 7
B:SNB:H:Op	Wi, Sp	24, 30	B:SNB:H:Tr	Wi, Sp	8, 24
R:SNB:H:Tr	Wi	5	B:SNB:M:Tr	Wi, Sp	9, 15
B:AF:H:Ri	Wi	17	B:AV:H:Tr	Wi, AS	3, 8

R:AV:H:Op	Wi	17	W:SNB:H:Tr	Wi	5, 5
R:SNB:H:Ri	Wi	52	B:SNB:VL:Tr	Wi	5
W:AV:H:Op	Sp	3	R:SNB:VL:Tr	Wi	6
R:AF:H:Op	Sp	5	R:AV:M;Tr	Sp	1
R:AF:H:Ri	Sp	10	R:SNB:H:Ri	Sp	34
R:SNB:VL:Tr	Sp	18	B:AV:M:Op	AS	1
B:SNB:VL:Tr	Sp	20	B:SNB:M;Op	AS	7
B:AV:VL:Op	AS	1			
R:SNB:VL:Op	AS	6			
B:SNB:VL:Op	AS	8			
B:SNB:H:Ri	AS	17			

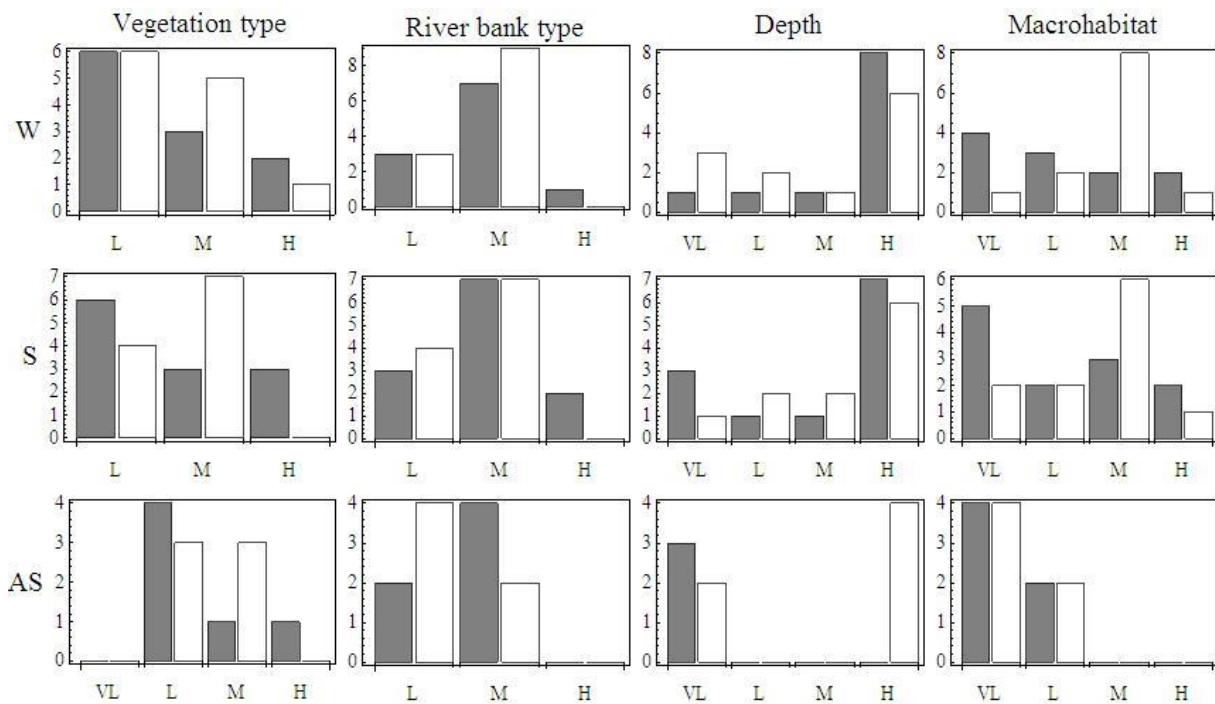


Figure A.1: Number of occurrences of each variable class in the antecedents of the C+ rules resulting of model C2 (two crisp sets indicating pike presence or absence) that predict pike presence (grey bars) and pike absence (white bars; winter (Wi), spring (Sp) and autumn-summer (AS)).

Table A.4: Final rule base of model C2 (two crisp sets indicating pike presence or absence). Black boxes indicate the output class. The rule antecedents are vegetation: bare (B), reedy (R) and woody (W); river bank type: vertically reinforced (AV), semi-natural (SNB) and artificial foreshore (AF); depth: very low (VL), low (L), medium (M) and high (H), macrohabitat type: open water (Op), riparian zone (Ri), tributary (Tr) and side arm (Sa), and season: winter (Wi), spring (Sp) and autumn-summer (AS).

Antecedent		Consequent
Vegetation:River bank type: Depth:Macrohabitat	Season	Pike presence (black) Pike absence (white)
B:AV:VL:Op	AS	
B:AV:VL:Tr	Sp	
B:AV:VL:Tr	Wi	
B:AV:M:Op	AS	
B:AV:M:Tr	Wi, Sp	

B:AV:H:Op	Wi, Sp, AS	
B:AV:H:Ri	Wi, Sp	
B:AV:H:Ri	Sp	
B:AV:H:Tr	Wi, AS	
B:SNB:VL:Op	AS	
B:SNB:VL:Ri	AS	
B:SNB:VL:Tr	Sp	
B:SNB:VL:Tr	Wi	
B:SNB:VL:Sa	Wi, Sp	
B:SNB:L:Op	AS	
B:SNB:L:Ri	AS	
B:SNB:L:Tr	Wi, Sp	
B:SNB:L:Sa	Wi, Sp	
B:AF:H:Op	Wi, Sp	
B:AF:H:Ri	Wi	
B:AF:H:Ri	Sp	
B:AF:H:Ri	AS	
B:R:H:Ri	Sp	
B:SNB:H:Op	Wi, Sp	
B:SNB:H:Op	AS	
B:SNB:H:Ri	AS	
B:SNB:H:Ri	Wi	
B:SNB:H:Tr	Wi, Sp	
B:SNB:M:Tr	Wi, Sp	
B:SNB:M;Op	AS	
R:AF:H:Op	Sp	
R:AF:H:Op	Wi	
R:AF:H:Op	AS	
R:AF:H:Ri	Sp	
R:AF:H:Ri	AS	
R:AF:H:Ri	Wi	
R:AV:H:Op	Wi	
R:AV:H:Op	Sp, AS	
R:AV:H:Ri	Wi, Sp, AS	
R:AV:M;Tr	Sp	
R:SNB:H:Op	Wi, Sp, AS	
R:SNB:H:Op	Wi, Sp	
R:SNB:H:Ri	Wi	
R:SNB:H:Ri	Sp	
R:SNB:H:Tr	Wi	
R:SNB:H:Tr	Sp	
R:SNB:L:Op	AS	
R:SNB:L:Tr	Wi, Sp	
R:SNB:M:Op	AS	
R:SNB:M:Tr	Sp	
R:SNB:M:Tr	Wi	
R:SNB:VL:Op	AS	
R:SNB:VL:Tr	Sp	

R:SNB:VL:Tr	Wi	
W:AV:H:Op	Sp	
W:AV:H:Op	Wi, AS	
W:AV:H:Ri	Sp	
W:AV:H:Ri	Wi	
W:AV:H:Tr	Sp	
W:SNB:H:Op	Wi, Sp	
W:SNB:H:Op	AS	
W:SNB:H:Ri	Wi, Sp, AS	
W:SNB:H:Tr	Wi	
W:SNB:H:Tr	Sp	

Table A.5: Rules that correctly predict pike absence in winter (Wi), spring (Sp) and autumn-summer (AS) in model C2, which is optimised based on the adjusted average deviation (aAD) and forced to overpredict by assigning a value of zero to α . The rule antecedents are vegetation: bare (B), reedy (R) and woody (W); river bank type: vertically reinforced (AV), semi-natural (SNB) and artificial foreshore (AF); depth: very low (VL), low (L), medium (M) and high (H) and macrohabitat type: open water (Op), riparian zone (Ri), tributary (Tr) and side arm (Sa).

Vegetation:River bank type: Depth:Macrohabitat	Season
B:AV:H:Tr	Wi, Sp
B:SNB:L:Tr	Wi, Sp
B:AF:H:Op	Sp
R:AV:M:Tr	Sp
R:SNB:VL:Sa	Sp
R:SNB:L:Tr	Sp
W:SNB:H:Tr	Sp
B:SNB:M:Tr	Wi, Sp
B:AV:VL:Tr	Sp
B:AV:VL:Tr	Wi
B:SNB:VL:Tr	Wi
B:SNB:H:Tr	Wi
B:AF:H:Op	Wi
R:SNB:VL:Tr	Wi
R:SNB:VL:Sa	Wi
R:SNB:L:Tr	Wi
R:SNB:M:Tr	Wi
W:SNB:H:Tr	Wi
B:AV:M:Op	AS
B:SNB:L:Op	AS
B:SNB:M:Op	AS
B:AF:H:Ri	AS
R:AV:H:Op	AS
R:AV:H:Ri	AS
R:SNB:L:Op	AS
R:SNB:M:Op	AS

References

- Aarestrup, K. (2009).** "Oceanic spawning migration of the European eel (*Anguilla anguilla*) (vol 325, pg 1660, 2009)." *Science* 326(5955): 936-936.
- Adriaenssens, V., B. De Baets, P. L. M. Goethals and N. De Pauw (2004a).** "Fuzzy rulebased models for decision support in ecosystem management." *Science of the Total Environment* 319: 1-12.
- Adriaenssens, V., P. L. M. Goethals, J. Charles and N. De Pauw (2004b).** "Application of Bayesian Belief Networks for the prediction of macroinvertebrate taxa in rivers." *Ann. Limnol. Int. J. Limn.* 40: 181-191.
- Adriaenssens, V., P. L. M. Goethals and N. De Pauw (2006).** "Fuzzy knowledge-based models for prediction of *Asellus* and *Gammarus* in watercourses in Flanders (Belgium)." *Ecological Modelling* 195: 3-10.
- Aebischer, N. J., P. A. Robertson and R. E. Kenward (1993).** "Compositional Analysis of Habitat Use from Animal Radio-Tracking Data." *Ecology* 74(5): 1313-1325.
- Aikake, H. (1974).** "New look at statistical-model identification." *IEEE Transactions on Automatic Control* 19: 716-723.
- Arlinghaus, R., S. Matsumura and U. Dieckmann (2009).** "Quantifying selection differentials caused by recreational fishing: development of modeling framework and application to reproductive investment in pike (*Esox lucius*)." *Evolutionary Applications* 2(3): 335-355.
- Arlinghaus, R., S. Matsumura and U. Dieckmann (2010).** "The conservation and fishery benefits of protecting large pike (*Esox lucius* L.) by harvest regulations in recreational fishing." *Biological Conservation* 143(6): 1444-1459.
- Baetens, J. M. (2012).** Discrete spatio-temporal modelling paradigms for environmental processes: SWOT analysis, application portfolio and Lyapunovian stability analysis. Bioscience Engineering. Ghent, Ghent University. PhD.
- Baktoft, H., K. Aarestrup, S. Berg, M. Boel, L. Jacobsen, N. Jepsen, A. Koed, J. C. Svendsen and C. Skov (2012).** "Seasonal and diel effects on the activity of northern pike studied by high-resolution positional telemetry." *Ecology of Freshwater Fish* 21(3): 386-394.
- Baltzer, H., W. P. Braun and W. Kohler (1998).** "Cellular automata models for vegetation dynamics." *Ecological Modelling* 107: 113-125.
- Bandini, S., G. Mauri, G. Pavesi and C. Simone (2000).** Parallel simulation of reaction-diffusion phenomena in percolation processes: A model based on a cellular automata. Future generation computer systems. Amsterdam, Elsevier.

- Bandini, S., G. Mauri and R. Serra (2001).** "Cellular automata: From a theoretical parallel computational model to its application to complex systems." *Parallel Computing* 27(5): 539-553.
- Baras, E. and J. Nindaba (1999).** "Seasonal and diel utilisation of inshore microhabitats by larvae and juveniles of *Leuciscus cephalus* and *Leuciscus leuciscus*." *Environmental Biology of Fishes* 56(1-2): 183-197.
- Barbaro, A., B. Einarsson, B. Birnir, S. Sigurosson, H. Valdimarsson, O. K. Palsson, S. Sveinbjornsson and P. Sigurosson (2009).** "Modelling and simulations of the migration of pelagic fish." *Ices Journal of Marine Science* 66(5): 826-838.
- Barredo, J. I., M. Kasanko, N. McCormick and C. Lavallo (2003).** "Modelling dynamic spatial processes: simulation of urban future scenarios through cellular automata." *Landscape and Urban Planning* 64(3): 145-160.
- Barry, S. and J. Elith (2006).** "Error and uncertainty in habitat models." *Journal of Applied Ecology* 43: 413-423.
- Bauer, S. and M. Klaassen (2013).** "Mechanistic models of animal migration behaviour their diversity, structure and use." *Journal of Animal Ecology* 82(3): 498-508.
- Beaudoin, C. P., W. M. Tonn, E. E. Prepas and L. I. Wassenaar (1999).** "Individual specialization and trophic adaptability of northern pike (*Esox lucius*): an isotope and dietary analysis." *Oecologia* 120(3): 386-396.
- Beaumont, W. R. C., B. Cresswell, K. H. Hodder, J. E. G. Masters and J. S. Welton (2002).** "A simple activity monitoring radio tag for fish." *Hydrobiologia* 483(1-3): 219-224.
- Beguer-Pon, M., J. Benchetrit, M. Castonguay, K. Aarestrup, S. E. Campana, M. J. W. Stokesbury and J. J. Dodson (2012).** "Shark Predation on Migrating Adult American Eels (*Anguilla rostrata*) in the Gulf of St. Lawrence." *Plos One* 7(10).
- Blecic, I., A. Borruso, A. Cecchini, A. D'Argenio, F. Montagnino and G. Trunfio, A. (2009).** "A cellular automata-ready GIS infrastructure for geosimulations and territorial analysis." *Proceedings of the 2nd International Conference on Computer Science and its Applications*. Kyung Hee University, Suwon, Korea.: 313-327. December.
- Bosworth, A. and J. M. Farrell (2006).** "Genetic divergence among northern pike from spawning locations in the upper St. Lawrence River." *North American Journal of Fisheries Management* 26(3): 676-684.
- Bry, C. (1996).** Role of vegetation in the life cycle of pike. Pike: Biology and exploitation. J. F. Craig. London, Chapman & Hall: 45-67.
- Burkholder, A. and D. R. Bernard (1994).** Movements and distribution of radio-tagged northern pike in Minto Flats. Fishery Manuscript. Anchorage USA, Alaska Department of Fish and Game. 94: 48.
- Burks, A. W. (1970).** Von Neumann's self-reproducing automata. Essays on cellular automata. A. W. Burks. Champaign, University of Illinois Press: 3-74.
- Burnham, K. P. and D. R. Anderson (2002).** Model selection and multimodel inference: a practical information-theoretic approach. New York, Springer-Verlag.
- Cagnacci, F., L. Boitani, R. A. Powell and M. S. Boyce (2010).** "Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges." *Philosophical Transactions of the Royal Society B-Biological Sciences* 365(1550): 2157-2162.
- Calenge, C. (2006).** "The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals." *Ecological Modelling* 197(3-4): 516-519.
- Camazine, S., J.-L. Deneubourg, N. R. Sneyd, G. Theraulaz and E. Bonabeau (2003).** Self-organisation in biological systems, Princeton University Press.
- Campbell, M. D., K. Rose, K. Boswell and J. Cowan (2011).** "Individual-based modeling of an artificial reef fish community: Effects of habitat quantity and degree of refuge." *Ecological Modelling* 222(23-24): 3895-3909.

- Casselman, J. M. (1978).** "Effects of environmental factors on growth, survival, activity and exploitation of northern pike." *Amer. Fish. Soc. Spec. Publ.* 11: 114-128.
- Casselman, J. M. and C. A. Lewis (1996).** "Habitat requirements for northern pike (*Esox lucius*)." *Canadian Journal for Fisheries and Aquatic Sciences* 53: 161-174.
- Castro-Santos, T. and A. Haro (2003).** "Quantifying migratory delay: a new application of survival analysis methods." *Canadian Journal of Fisheries and Aquatic Sciences* 60: 986-996.
- Caswell, H., Ed. (2001).** Matrix population models, second ed. Sinauer Associates. Sunderland, USA.
- Catalano, M. J. and M. S. Allen (2010).** "A size- and age-structured model to estimate fish recruitment, growth, mortality, and gear selectivity." *Fisheries Research* 105(1): 38-45.
- Chapman, C. A. and W. C. Mackay (1984a).** "Direct Observation of Habitat Utilization by Northern Pike." *Copeia* 1984(1): 255-258.
- Chapman, C. A. and W. C. Mackay (1984b).** "Versatility in Habitat Use by a Top Aquatic Predator, *Esox lucius* L." *Journal of Fish Biology* 25(1): 109-115.
- Chapman, D. W. (1968).** Production. Methods for assessment of fish production in fresh waters. W. D. Ricker. Oxford and Edinburgh, Blackwell scientific publications: 182-196.
- Chapman, L. J. and W. C. Mackay (1990).** "Ecological Correlates of Feeding Flexibility in Northern Pike (*Esox-Lucius*)." *Journal of Freshwater Ecology* 5(3): 313-322.
- Chapman, L. J., W. C. Mackay and C. W. Wilkinson (1989).** "Feeding Flexibility in Northern Pike (*Esox-Lucius*) - Fish Versus Invertebrate Prey." *Canadian Journal of Fisheries and Aquatic Sciences* 46(4): 666-669.
- Charles, S., F. Subtil, J. Kielbassa and D. Pont (2008).** "An individual-based model to describe a bullhead population dynamics including temperature variations." *Ecological Modelling* 215(4): 377-392.
- Chen, Q. W., R. Han, F. Ye and W. F. Li (2011).** "Spatio-temporal ecological models." *Ecological Informatics* 6(1): 37-43.
- Chen, Q. W. and A. E. Mynett (2003).** "Effects of cell size and configuration in cellular automata based prey-predator modelling." *Simulation Modelling Practice and Theory* 11(7-8): 609-625.
- Chen, Q. W. and A. E. Mynett (2006).** "Modelling algal blooms in the Dutch coastal waters by integrated numerical and fuzzy cellular automata approaches." *Ecological Modelling* 199(1): 73-81.
- Chen, Y., X. Li, X. Liu and B. Ai (2014).** "Modeling urban land-use dynamics in a fast developing city using the modified logistic cellular automaton with a patch-based simulation strategy." *International Journal of Geographical Information Science* 28(2): 234-255.
- Chen, Z., L. Zhao and K. Lee (2010).** "Environmental risk assessment of offshore produced water discharges using a hybrid fuzzy-stochastic modeling approach." *Environmental Modelling & Software* 25(6): 782-792.
- CIW (2010).** Stroomgebiedsplan voor de Schelde 2010-2015, Commissie Integraal Waterbeleid.
- Claessen, D., C. Van Oss, A. M. de Roos and L. Persson (2002).** "The impact of size-dependent predation on population dynamics and individual life history." *Ecology* 83(6): 1660-1675.
- Clark, M. E. and K. A. Rose (1997a).** "Factors affecting competitive dominance of rainbow trout over brook trout in southern Appalachian streams: Implications of an individual-based model." *Transactions of the American Fisheries Society* 126(1): 1-20.
- Clark, M. E. and K. A. Rose (1997b).** "Individual-based model of stream-resident rainbow trout and brook char: Model description, corroboration, and effects of sympatry and spawning season duration." *Ecological Modelling* 94(2-3): 157-175.
- Codd, E. F. (1968).** Cellular automata. New York, Academic Press.

- Codling, E. A., M. J. Plank and S. Benhamou (2008).** "Random walk models in biology." *Journal of the Royal Society Interface* 5(25): 813-834.
- Coeck, J. (2002).** Het verschijnsel vismigratie in Vlaamse waterlopen. Referaat Studiedag Vismigratie, 14 juni 2000, Instituut voor Natuur- en Bosonderzoek: 1-11.
- Cohen, J. (1960).** "A coefficient of agreement for nominal scales." *Educational and Psychological Measurement* 20: 37-46.
- Cook, M. F. and E. P. Bergersen (1988).** "Movements, Habitat Selection, and Activity Periods of Northern Pike in 11 Mile Reservoir, Colorado." *Transactions of the American Fisheries Society* 117(5): 495-502.
- Cooke, S. J., S. G. Hinch, M. Wikelski, R. D. Andrews, L. J. Kuchel, T. G. Wolcott and P. J. Butler (2004).** "Biotelemetry: a mechanistic approach to ecology." *Trends in Ecology & Evolution* 19(6): 334-343.
- Cooper, J. E., J. V. Mead, J. M. Farrel and R. G. Werner (2008).** "Potential effects of spawning habitat changes on the segregation of northern pike (*Esox lucius*) and muskellunge (*E. masquinongy*) in the Upper St. Lawrence River." *Hydrobiologia* 601: 41-53.
- Copp, G. H. (1992).** "Comparative Microhabitat Use of Cyprinid Larvae and Juveniles in a Lotic Floodplain Channel." *Environmental Biology of Fishes* 33(1-2): 181-193.
- Costa, R. M. S., F. Martinez-Capel, R. Munoz-Mas, J. D. Alcaraz-Hernandez and V. Garofano-Gomez (2012).** "Habitat Suitability Modelling at Mesohabitat Scale and Effects of Dam Operation on the Endangered Jucar Nase, *Parachondrostoma Arrigonis* (River Cabriel, Spain)." *River Research and Applications* 28(6): 740-752.
- Craig, J. F., Ed. (1996).** Pike: Biology and Exploitation. London, UK, Chapman & Hall.
- Craig, J. F. (2008).** "A short review of pike ecology." *Hydrobiologia* 601: 5-16.
- Craig, J. F. and C. Kipling (1983).** "Reproduction Effort Versus the Environment - Case-Histories of Windermere Perch, *Perca-Fluviatilis* L, and Pike, *Esox-Lucius* L." *Journal of Fish Biology* 22(6): 713-727.
- Crook, D. A., A. I. Robertson, A. J. King and P. Humphries (2001).** "The influence of spatial scale and habitat arrangement on diel patterns of habitat use by two lowland river fishes." *Oecologia* 129: 525-533.
- D'heygere, T., G. P.L.M. and N. De Pauw (2003).** "Use of genetic algorithms to select input variables in decision tree models for the prediction of benthic macroinvertebrates." *Ecological Modelling* 160: 291-300.
- D'heygere, T., G. P.L.M. and N. De Pauw (2006).** "Genetic algorithms for optimisation of predictive ecosystems models based on decision trees and neural networks." *Ecological Modelling* 195: 20-29.
- Das Mahapatra, K., B. Gjerde, P. V. G. K. Reddy, M. Sahoo, R. K. Jana, J. N. Saha and M. Rye (2001).** "Tagging: on the use of passive integrated transponder (PIT) tags for the identification of fish." *Aquaculture Research* 32(1): 47-50.
- Dawson, F. H., E. M. F. Clinton and M. Ladle (1991).** "Macroinvertebrates on cut weed removed during weed-cutting operations along an English River, the River Frome, Dorset." *Aquaculture and fisheries management* 22: 113-122.
- De Laak, G. A. J. and W. A. M. van Emmerik, Eds. (2006).** Kennisdocument snoek, *Esox lucius* (Linnaeus, 1758). Kennisdocument, Sportvisserij Nederland, Bilthoven.
- De Nayer, B. and C. Belpaire (1997).** "De visfauna op de IJzer in 1996." *Water* 97: 291-300.
- De Nie, H. W., Ed. (1996).** Atlas van de nederlandse zoetwatervissen Doetinchem, The Netherlands, Stichting atlas verspreiding nederlandse zoetwatervissen, Media Publishing.
- De Rycke, A. A., I. I. Verelst, K. K. Decler, P. Adriaens, K. Devos, L. Debruyne, P. Quataert, S. Lammens and E. Ghyselbrecht (2006).** Evaluatie van NTMB-projecten langs de IJzer uitgevoerd door W&Z (AWZ/WWK) : tussentijds verslag : waterkwaliteit, vegetatie, broedvogels (gegevens van 2005). Brussel, Instituut voor Natuur- en Bosonderzoek.

- Dedecker, A. P., P. L. M. Goethals, T. D'heygere, T. Gevrey, S. Leks and N. De Pauw (2005).** "Application of artificial neural network models to analyse the relationships between *Gammarus pulex* L. (Crustacea, Amphipoda) and river characteristics." *Environmental Modelling and Software* 111: 223-241.
- Dedecker, A. P., P. L. M. Goethals, W. Gabriels and N. De Pauw (2004).** "Optimization of Artificial Neural Network (ANN) model design for prediction of macroinvertebrates in the Zwalm river basin (Flanders, Belgium)." *Ecological Modelling* 174: 161-173.
- Diana, J. S. (1979).** "Feeding Pattern and Daily Ration of a Top Carnivore, the Northern Pike (*Esox-Lucius*)." *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 57(11): 2121-2127.
- Diana, J. S. (1980).** "Diel Activity Pattern and Swimming Speeds of Northern Pike (*Esox-Lucius*) in Lac Ste Anne, Alberta." *Canadian Journal of Fisheries and Aquatic Sciences* 37(9): 1454-1458.
- Diana, J. S. (1983).** "An Energy Budget for Northern Pike (*Esox lucius*)." *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 61(9): 1968-1975.
- Diana, J. S., W. C. Mackay and M. Ehrman (1977).** "Movements and Habitat Preference of Northern Pike (*Esox-Lucius*) in Lac Ste Anne, Alberta." *Transactions of the American Fisheries Society* 106(6): 560-565.
- Dillane, E., P. McGinnity, J. P. Coughlan, M. C. Cross, E. de Eyto, E. Kenchington, P. Prodohl and T. F. Cross (2008).** "Demographics and landscape features determine intrariver population structure in Atlantic salmon (*Salmo salar* L.): the case of the River Moy in Ireland." *Molecular Ecology* 17(22): 4786-4800.
- Donnelly, R. E., J. M. Caffrey and D. M. Tierney (1998).** "Movement of bream (*Abramis brama* (L.)), rudd x bream hybrid, tench (*Tinca tinca* (L.)) and pike (*Esox lucius* (L.)) in an Irish canal habitat." *Hydrobiologia* 371/372: 305-308.
- Dumortier, M., L. De Bruyn, M. Hens, J. Peymen, A. Schneiders, T. Van Daele and W. Van Reeth (2009).** Natuurrapport Vlaanderen. Natuurverkenning 2030. Brussel, Instituut voor Natuur- en Bosonderzoek: 224.
- Dunbar, M. J., K. Alfredsen and A. Harby (2012).** "Hydraulic-habitat modelling for setting environmental river flow needs for salmonids." *Fisheries Management and Ecology* 19(6): 500-517.
- Edeline, E., T. O. Haugen, F. A. Weltzien, D. Claessen, I. J. Winfield, N. C. Stenseth and L. A. Vollestad (2010).** "Body downsizing caused by non-consumptive social stress severely depresses population growth rate." *Proceedings of the Royal Society B-Biological Sciences* 277(1683): 843-851.
- Eide, A. (2011).** On the limits of improved fish finding capacity and its contribution to resource conservation. 19th international congress on modelling and simulation, 12-16 December 2011, Perth, Australia.
- Eklöv, P. (1992).** "Group foraging versus solitary foraging efficiency in piscivorous predators: the perch, *Perca fluviatilis*, and pike, *Esox lucius*, patterns." *Animal Behaviour* 44(2): 313-326.
- Eklöv, P. (1997).** "Effect of habitat complexity and prey abundance on the spatial and temporal distribution of perch (*Perca fluviatilis*) and pike (*Esox lucius*)." *Can. J. Fish. Aquat. Sci.* 54(7): 1520-1531.
- Engstrom-Ost, J., M. Lehtiniemi, S. H. Jonasdottir and M. Viitasalo (2005).** "Growth of pike larvae (*Esox lucius*) under different conditions of food quality and salinity." *Ecology of Freshwater Fish* 14(4): 385-393.
- Estrada, A., R. Real and J. M. Vargas (2008).** "Using crisp and fuzzy modelling to identify favourability hotspots useful to perform gap analysis." *Biodiversity and Conservation* 17(4): 857-871.

- EU (2000).** EC Water Framework Directive. Official Journal of the European Communities. Brussels, Belgium, European Commission.
- Farrell, J. M. (2001).** "Reproductive success of sympatric northern pike and muskellunge in an upper St. Lawrence River Bay." *Transactions of the American Fisheries Society* 130(5): 796-808.
- Farrell, J. M., J. V. Mead and B. A. Murry (2006).** "Protracted spawning of St Lawrence River northern pike (*Esox lucius*): simulated effects on survival, growth, and production." *Ecology of Freshwater Fish* 15(2): 169-179.
- Farrell, J. M., B. A. Smith, H. B. Underwood and S. J. Smith (2007).** "Year-class formation of upper St. Lawrence River northern pike." *North American Journal of Fisheries Management* 27(2): 481-491.
- Farrell, J. M., R. G. Werner, S. R. LaPan and K. A. Claypoole (1996).** "Egg distribution and spawning habitat of northern pike and muskellunge in a St Lawrence River Marsh, New York." *Transactions of the American Fisheries Society* 125(1): 127-131.
- Ferreri, L. and E. Venturino (2013).** "Cellular automata for contact ecoepidemic processes in predator-prey systems." *Ecological Complexity* 13: 8-20.
- Fielding, A. H. and J. F. Bell (1997).** "A review of methods for the assessment of prediction errors in conservation presence/absence models." *Environmental Conservation* 24: 38-49.
- Flinders, J. M. and S. A. Bonar (2008).** "Growth, condition, diet, and consumption rates of northern pike in three Arizona reservoirs." *Lake and Reservoir Management* 24(2): 99-111.
- Frank, B. M., J. J. Piccolo and P. V. Baret (2011).** "A review of ecological models for brown trout: towards a new demogenetic model." *Ecology of Freshwater Fish* 20(2): 167-198.
- Fransen, B. R., S. D. Duke, L. G. McWethy, J. K. Walter and R. E. Bilby (2006).** "A logistic regression model for predicting the upstream extent of fish occurrence based on geographical information systems data." *North American Journal of Fisheries Management* 26: 960-975.
- Fresnadillo Martinez, M. J., E. Garcia Merino, E. Garcia Sanchez, J. E. Garcia Sanchez, A. Martin del Rey and G. Rodriguez Sanchez (2013).** "A Graph Cellular Automata Model to Study the Spreading of an Infectious Disease." *Advances in Artificial Intelligence. 11th Mexican International Conference on Artificial Intelligence, MICAI 2012. Revised Selected Papers*: 458-468.
- Fukuda, S. (2009).** "Consideration of fuzziness: Is it necessary in modelling fish habitat preference of Japanese medaka (*Oryzias latipes*)?" *Ecological Modelling* 220(21): 2877-2884.
- Galuardi, B. and M. Lutcavage (2012).** "Dispersal Routes and Habitat Utilization of Juvenile Atlantic Bluefin Tuna, *Thunnus thynnus*, Tracked with Mini PSAT and Archival Tags." *Plos One* 7(5).
- Gelowitz, C. M., A. Mathis and R. J. F. Smith (1993).** "Chemosensory Recognition of Northern Pike (*Esox-Lucius*) by Brook Stickleback (*Culaea Inconstans*) - Population Differences and the Influence of Predator Diet." *Behaviour* 127: 105-118.
- Gillenwater, D., T. Granata and U. Zika (2006).** "GIS-based modeling of spawning habitat suitability for walleye in the Sandusky River, Ohio, and implications for dam removal and river restoration." *Ecological Engineering* 28(3): 311-323.
- Giske, J., G. Huse and O. Fiksen (1998).** "Modelling spatial dynamics of fish." *Reviews in Fish Biology and Fisheries* 8: 57-91.
- Giske, J., M. Mangel, P. Jakobsen, G. Huse, C. Wilcox and E. Strand (2003).** "Explicit trade-off rules in proximate adaptive agents." *Evolutionary Ecology Research* 5(6): 835-865.
- Glasbergen, M. J. (2001).** Fish habitat requirements in the Dutch part of the River Rhine. Delft, WL/Delft Hydraulics Project Report: 49.
- Goethals, P. L. M., R. Zarkami, T. D'heygere, N. De Pauw, N. Jaarsma, M. Klinge, M. Grimm, G. Van Thuyne and C. Belpaire (2006).** Status, ecologie en bescherming van de

- snoek (*Esox lucius*) in Vlaanderen. Gent, Ministerie van de Vlaamse Gemeenschap. Eindrapport TWOL Project nr. B1G/14/2001, studie in opdracht van AMINAL, Afdeling Bos&Groen. Universiteit Gent: 111.
- Gomezuchida, D. (2009).** "Interaction of landscape and life history attributes on genetic diversity, neutral divergence and gene flow in a pristine community of salmonids." *Molecular Ecology* 18(23): 4854-4869.
- González, F., D. Dasgupta and L. F. Nino (2003).** A randomized real-valued negative selection algorithm. 2nd international conference on artificial immune systems, Edinburgh, United Kingdom.
- Goodwin, R. A., J. M. Nestler, J. J. Anderson, L. J. Weber and D. P. Loucks (2006).** "Forecasting 3-D fish movement behavior using a Eulerian-Lagrangian-agent method (ELAM)." *Ecological Modelling* 192(1-2): 197-223.
- Gregori, D., P. Berchialla and F. Foltran (2010).** "Comparing Bayesian Network, Artificial Neural Networks, Classification Trees and Classical Logistic Models in Quantitative Risk Assessment: An Application to the European Registry of Foreign Body Injuries in Children." *Injury Prevention* 16: A216-A216.
- Grimm, M. P. and M. Klinge (1996).** Pike and some aspects of its dependence on vegetation. Pike: Biology and Exploitation. J. F. Craig. London, UK, Chapman & Hall.
- Grimm, V. and S. Railsback (2005).** Individual-based modeling and ecology, Princeton University Press.
- Grimm, V., T. Wyszomirski, D. Aikman and J. Uchmanski (1999).** "Individual-based modelling and ecological theory: synthesis of a workshop." *Ecological Modelling* 115(2-3): 275-282.
- Guay, J. C., D. Boisclair, D. Rioux, M. Leclerc, M. Lapointe and P. Legendre (2000).** "Development and validation of numerical habitat models for juveniles of Atlantic salmon (*Salmo salar*)." *Canadian Journal of Fisheries and Aquatic Sciences* 57(10): 2065-2075.
- Guillaume, S. (2001).** "Designing fuzzy inference systems from data: An interpretability-oriented review." *Ieee Transactions on Fuzzy Systems* 9(3): 426-443.
- Guisan, A. and N. E. Zimmermann (2000).** "Predictive habitat distribution models in ecology." *Ecological Modelling* 135(2-3): 147-186.
- Gurkan, Z., A. Christensen, M. Maar, E. F. Moller, K. S. Madsen, P. Munk and H. Mosegaard (2013).** "Spatio-temporal dynamics of growth and survival of Lesser Sandeel early life-stages in the North Sea: Predictions from a coupled individual-based and hydrodynamic-biogeochemical model." *Ecological Modelling* 250: 294-306.
- Gurkan, Z., A. Christensen, M. van Deurs and H. Mosegaard (2012).** "Growth and survival of larval and early juvenile Lesser Sandeel in patchy prey field in the North Sea: An examination using individual-based modeling." *Ecological Modelling* 232: 78-90.
- Gurney, W. S. C. and R. M. Nisbet (1998).** Ecological dynamics, Oxford University Press inc.
- Haas, H. L., K. A. Rose, B. Fry, T. J. Minello and L. P. Rozas (2004).** "Brown shrimp on the edge: Linking habitat to survival using an individual-based simulation model." *Ecological Applications* 14(4): 1232-1247.
- Hammerschlag, N., A. J. Gallagher and D. M. Lazarre (2011).** "A review of shark satellite tagging studies." *Journal of Experimental Marine Biology and Ecology* 398(1-2): 1-8.
- Harris, J. W. and H. Stocker (1998).** Handbook of mathematics and computational science. New York, United States, Springer.
- Harvey, B. (2009).** A biological synopsis of northern pike (*Esox lucius*), Canadian Manuscript Report 2885, Fisheries and Aquatic Sciences.

- Harvey, B. C. and S. F. Railsback (2009).** "Exploring the Persistence of Stream-Dwelling Trout Populations under Alternative Real-World Turbidity Regimes with an Individual-Based Model." *Transactions of the American Fisheries Society* 138(2): 348-360.
- Hastie, T. and R. J. Tibshirani (1990).** Generalized additive models. London, Chapman and Hall.
- Haugen, T. O., I. J. Winfield, L. A. Vollestad, J. M. Fletcher, J. B. James and N. C. Stenseth (2006).** "The ideal free pike: 50 years of fitness-maximizing dispersal in Windermere." *Proceedings of the Royal Society B-Biological Sciences* 273(1604): 2917-2924.
- Hawkins, L. A., J. D. Armstrong and A. E. Magurran (2003).** "Settlement and habitat use by juvenile pike in early winter." *Journal of Fish Biology* 63: 174-186.
- Hayes, D., M. Jones, N. Lester, C. Chu, S. Doka, J. Netto, J. Stockwell, B. Thompson, C. K. Minns, B. Shuter and N. Collins (2009).** "Linking fish population dynamics to habitat conditions: insights from the application of a process-oriented approach to several Great Lakes species." *Reviews in Fish Biology and Fisheries* 19(3): 295-312.
- Hedger, R. D., L. E. Sundt-Hansen, T. Forseth, O. H. Diserud, O. Ugedal and A. G. Finstad (2013).** "Modelling the complete life-cycle of Atlantic salmon (*Salmo salar* L.) using a spatially explicit individual-based approach." *Ecological Modelling* 248: 119-129.
- Hobbs, N. T. and D. C. Bowden (1982).** "Confidence-Intervals on Food Preference Indexes." *Journal of Wildlife Management* 46(2): 505-507.
- Hogeweg, P. (1988).** "Cellular Automata as a Paradigm for Ecological Modeling." *Applied Mathematics and Computation* 27(1): 81-100.
- Holland, L. and M. Huston (1984).** "Relationship of young-of-the-year northern pike to aquatic vegetation types in backwaters of the Upper Mississippi River." *North American Journal of Fisheries Management* 4(4B): 514-522.
- Hubbard, S., P. Babak, S. T. Sigurdsson and K. G. Magnusson (2004).** "A model of the formation of fish schools and migrations of fish." *Ecological Modelling* 174(4): 359-374.
- Hüllermeier, E. (2005).** "Fuzzy methods in machine learning and data mining: Status and prospects." *Fuzzy Sets and Systems* 156: 387-406.
- Humphries, N. E., N. Queiroz, J. R. M. Dyer, N. G. Pade, M. K. Musyl, K. M. Schaefer, D. W. Fuller, J. M. Brunnschweiler, T. K. Doyle, J. D. R. Houghton, G. C. Hays, C. S. Jones, L. R. Noble, V. J. Wearmouth, E. J. Southall and D. W. Sims (2010).** "Environmental context explains Levy and Brownian movement patterns of marine predators." *Nature* 465(7301): 1066-1069.
- Huse, G. and I. Ellingsen (2008).** "Capelin migrations and climate change - a modelling analysis." *Climatic Change* 87(1-2): 177-197.
- Huse, G. and J. Giske (1998).** "Ecology in Mare Pentium: an individual-based spatio-temporal model for fish with adapted behaviour." *Fisheries Research* 37(1-3): 163-178.
- Inskip, P. D. (1982).** Habitat suitability index models: Northern Pike, U.S. Department of the Interior, Fisheries and Wildlife Service, FWS/OB-82/10.17: 40.
- Jacobsen, L., M. Andersen, P. Gronkjaer and C. Skov (2008).** "Turbidity increases behavioural diversity in northern pike, *Esox lucius* L., during early summer." *Fisheries Management and Ecology* 15(5-6): 377-383.
- Jacobsen, L., C. Skov, A. Koed and S. Berg (2007).** "Short-term salinity tolerance of northern pike, *Esox lucius*, fry, related to temperature and size." *Fisheries Management and Ecology* 14(5): 303-308.
- Jepsen, N., S. Beck, C. Skov and A. Koed (2001).** "Behavior of pike (*Esox lucius* L.) > 50 cm in a turbid reservoir and in a clearwater lake." *Ecology of Freshwater Fish* 10(1): 26-34.
- Jepsen, N., A. Koed, E. B. Thorstad and E. Baras (2002).** "Surgical implantation of telemetry transmitters in fish: how much have we learned?" *Hydrobiologia* 483(1-3): 239-248.

- Jimenez, A. (2013).** "Cellular automata to describe seismicity: A review." *Acta Geophysica* 61(6): 1325-1350.
- Johnson, D. H. (1980).** "The comparison of usage and availability measurements for evaluating resource preference." *Ecology* 61: 65-71.
- Jones, D. R., J. W. Kiceniuk and O. S. Bamford (1974).** "Evaluation of the swimming performance of several fish species from the Mackenzie River." *Journal of Fish Research Board Canada* 31: 1641-1647.
- Kahilainen, K. and H. Lehtonen (2003).** "Piscivory and prey selection of four predator species in a whitefish dominated subarctic lake." *Journal of Fish Biology* 63(3): 659-672.
- Kampichler, C., J. Barthel and R. Wieland (2000).** "Species density of foliage-dwelling spiders in field margins: a simple, fuzzy rule-based model." *Ecological Modelling* 129(1): 87-99.
- Kampichler, C., R. Wieland, S. Calme, H. Weissenberger and S. Arriaga-Weiss (2010).** "Classification in conservation biology: A comparison of five machine-learning methods." *Ecological Informatics* 5(6): 441-450.
- Katajisto, J. and A. Moilanen (2006).** "Kernel-based home range method for data with irregular sampling intervals." *Ecological Modelling* 194(4): 405-413.
- Keinanen, M., S. Peuranen, M. Nikinmaa, C. Tigerstedt and P. J. Vuorinen (2000).** "Comparison of the responses of the yolk-sac fry of pike (*Esox lucius*) and roach (*Rutilus rutilus*) to low pH and aluminium: sodium influx, development and activity." *Aquatic Toxicology* 47(3-4): 161-179.
- Kenward, R. E. (2000).** A manual for wildlife radio tagging, Academic Press.
- Kerle, F., F. Zollner, B. Kappus, W. Marx and J. Giesecke (2001).** Fish habitats and vegetation modelling in floodplains with CASIMIR. Stuttgart, Germany, CFR project report 13, IWS, University of Stuttgart: 75.
- Kerr, L. A., S. X. Cadrin and D. H. Secor (2010).** "The role of spatial dynamics in the stability, resilience, and productivity of an estuarine fish population." *Ecological Applications* 20(2): 497-507.
- Kilfoyle, D. B. and A. B. Baggeroer (2000).** "The state of the art in underwater acoustic telemetry." *Ieee Journal of Oceanic Engineering* 25(1): 4-27.
- Kiplig, C. and W. E. Frost (1970).** "A study of mortality, population numbers, year class strengths, production and food consumption of pike, *Esox lucius* L., in Windermere from 1944 to 1962." *Journal of Animal Ecology* 39: 115-157.
- Kipling, C. and W. E. Frost (1970).** "A Study of Mortality, Population Numbers, Year Class Strengths, Production and Food Consumption of Pike, *Esox-Lucius* L, in Windermere from 1944 to 1962." *Journal of Animal Ecology* 39(1): 115-&.
- Kirkpatrick, S., C. D. Gelatt and M. P. Vecchi (1983).** "Optimization by Simulated Annealing." *Science* 220(4598): 671-680.
- Knight, C. M., R. E. Gozlan and M. C. Lucas (2008).** "Can seasonal home-range size in pike *Esox lucius* predict excursion distance?" *Journal of Fish Biology* 73(4): 1058-1064.
- Kobler, A., T. Klefoth and R. Arlinghaus (2008a).** "Site fidelity and seasonal changes in activity centre size of female pike *Esox lucius* in a small lake." *Journal of Fish Biology* 73(3): 584-596.
- Kobler, A., T. Klefoth, C. Wolter, F. Fredrich and R. Arlinghaus (2008b).** "Contrasting pike (*Esox lucius* L.) movement and habitat choice between summer and winter in a small lake." *Hydrobiologia* 601: 17-27.
- Koed, A., K. Balleby, P. Mejlhede and K. Aarestrup (2006).** "Annual movement of adult pike (*Esox lucius* L.) in a lowland river." *Ecology of Freshwater Fish* 15(2): 191-199.

- Koehn, J. D., J. H. Eiler, J. A. McKenzie and W. G. O'Connor (2012).** "An Improved Method for Obtaining Fine-Scale Location of Radio Tags when Tracking by Boat." *Advances in Fish Tagging and Marking Technology* 76: 379-384.
- Kottelat, M. and J. Freyhof (2007).** Handbook of European freshwater fishes. Cornol, Switzerland, Publications Kottelat.
- Landuyt, D., S. Broekx, R. D'Hondt, G. Engelen, J. Aertsens and P. L. M. Goethals (2013).** "A review of bayesian belief networks in ecosystem service modelling." *Environmental Modelling and Software* 46: 1-11.
- Le Fur, J. and P. Simon (2009).** "A new hypothesis concerning the nature of small pelagic fish clusters: An individual-based modelling study of *Sardinella aurita* dynamics off West Africa." *Ecological Modelling* 220(9-10): 1291-1304.
- Lehtiniemi, M., J. Engstrom-Ost and M. Viitasalo (2005).** "Turbidity decreases anti-predator behaviour in pike larvae, *Esox lucius*." *Environmental Biology of Fishes* 73(1): 1-8.
- Lek, S. and J. F. Guegan (1999).** "Artificial neural networks as a tool in ecological modelling, an introduction." *Ecological Modelling* 120(2-3): 65-73.
- Li, H. (2009).** Spatial pattern dynamics in aquatic ecosystem modelling. Delft University of Technology. Delft, University of Delft: 181.
- Li, W. F., R. Han, Q. W. Chen, S. Qu and Z. N. Cheng (2010).** "Individual-based modelling of fish population dynamics in the river downstream under flow regulation." *Ecological Informatics* 5(2): 115-123.
- Li, X. and A. Gar-On Yeh (2000).** "Modelling sustainable urban development by the integration of constrained cellular automata and GIS." *International Journal of Geographical Information Science* 14: 131-152.
- Liebowitz, J. (1998).** Handbook of applied expert systems. Boca Raton, FL, CRC Press.
- Limburg, K. E. and L. Westin (2002).** "Newly discovered reproductive isolation reveals sympatric populations of *Esox lucius* in the Baltic." *Journal of Fish Biology* 61(6): 1647-1652.
- Liu, K. F. R. and C. W. Yu (2009).** "Integrating case-based and fuzzy reasoning to qualitatively predict risk in an environmental impact assessment review." *Environmental Modelling & Software* 24(10): 1241-1251.
- Lucas, M. C. (1992).** "Spawning Activity of Male and Female Pike, *Esox-Lucius* L, Determined by Acoustic Tracking." *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 70(1): 191-196.
- Lucas, M. C., E. Baras, T. Thom, A. Duncan and O. Slavik (2001).** Migration of freshwater fishes. Oxford, UK, Blackwell Science Ltd.
- MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson and A. B. Franklin (2003).** "Estimating site occupancy, colonization and local extinction when a species is detected imperfectly." *Ecology* 84: 2200-2207.
- Maeckelberghe, H. (2002).** De kwaliteit van het Vlaamse oppervlaktewater en de afvalwaterlozingen in 2002. Een toelichting bij de resultaten van de meetnetten van de Vlaamse Milieumaatschappij, Report of the Flemish Environment Agency (VMM).
- Maes, G. E., J. K. J. Van Houdt, K. D. Gelas, D. D. Charleroy and F. A. M. Volckaert (2004).** Conservatiegenetische aspecten van het beheer van snoek (*Esox lucius*) in Europa en Vlaanderen: opvolging van natuurlijke en gekweekte Vlaamse populaties. Tech. report, Instituut voor bosbouw en wildbeheer.
- Magnússon, K. G., S. Sigurdsson and B. Einarsson (2004).** A discrete and stochastic simulation model for migration of with application to capelin in the seas around Iceland. Technical Report.
- Maitland, P. S. and R. N. Campbell (1993).** Freshwater fishes. London, United Kingdom, Collins.

- Malinin, L. K. (1969).** "Home range and homing instinct of fish." *Zoologicheskij Zhurnal* 48: 381-391.
- Malinin, L. K. (1970).** "The use of ultrasonic transmitters for the marking of bream and pike." *Biologiya Vnutrennikh Vod: Informatsionnyi Byulleten* 8: 75-78.
- Manly, B. F. J. (2002).** Resource selection by animals: statistical design and analysis for field studies. Dordrecht, The Netherlands., Kluwer.
- Manly, B. F. J., L. McDonald and D. Thomas (1993).** Resource selection by animals: statistical design and analysis for field studies. London, UK, Chapman & Hall.
- Margenau, T. L., S. P. AveLallemant, D. Giebtbrock and S. T. Schram (2008).** "Ecology and management of northern pike in Wisconsin." *Hydrobiologia* 601: 111-123.
- Marshall, A., J. S. Mills, K. L. Rhodes and J. McIlwain (2011).** "Passive acoustic telemetry reveals highly variable home range and movement patterns among unicornfish within a marine reserve." *Coral Reefs* 30(3): 631-642.
- Masters, J. E. G., K. H. Hodder, W. R. C. Beaumont, R. E. Gozlan, A. C. Pinder, R. E. Kenward and J. S. Welton (2003).** Spatial behaviour of pike *Esox lucius* L. in the River Frome, UK. Fifth Conference on Fish Telemetry held in Europe., Italy.
- Masters, J. E. G., J. S. Welton, W. R. C. Beaumont, K. H. Hodder, A. C. Pinder, R. E. Gozlan and M. Ladle (2002).** "Habitat utilisation by pike *Esox lucius* L. during winter floods in a southern English chalk river." *Hydrobiologia* 483(1-3): 185-191.
- Mcdowall, R. M. (1993).** "Implications of Diadromy for the Structuring and Modeling of Riverine Fish Communities in New-Zealand." *New Zealand Journal of Marine and Freshwater Research* 27(4): 453-462.
- Meixler, M., M. Bain and M. Todd Walter (2009).** "Predicting barrier passage and habitat suitability for migratory fish species." *Ecological Modelling* 220(20): 2782-2791.
- Melia, P., M. Schiavina, M. Gatto, L. Bonaventura, S. Masina and R. Casagrandi (2013).** "Integrating field data into individual-based models of the migration of European eel larvae." *Marine Ecology Progress Series* 487: 135-149.
- Miller, C. S., M. Hebblewhite, J. M. Goodrich and D. G. Miquelle (2010).** "Review of research methodologies for tigers: Telemetry." *Integrative Zoology* 5(4): 378-389.
- Miller, L. M., L. Kallemeyn and W. Senanan (2001).** "Spawning-site and natal-site fidelity by northern pike in a large lake: Mark-recapture and genetic evidence." *Transactions of the American Fisheries Society* 130(2): 307-316.
- Mingelbier, M., P. Brodeur and J. Morin (2008).** "Spatially explicit model predicting the spawning habitat and early stage mortality of Northern pike (*Esox lucius*) in a large system: the St. Lawrence River between 1960 and 2000." *Hydrobiologia* 601(1): 55-69.
- Minns, C. K., R. G. Randall, J. E. Moore and V. W. Cairns (1996).** "A model simulating the habitat supply limits on northern pike, *Esox lucius*, in Hamilton harbour, Lake Ontario " *Canadian Journal of Fisheries and Aquatic Sciences* 53(1): 20-34.
- Minss, A. W., A. E. Mynett, Q. Chen and H. F. P. van den Boogaard (2000).** "A Cellular Automata Approach to Ecological Modelling." In: *Odgaard, A.J. (Ed.). Proceedings of Hydroinformatics Conference 2000, Iowa, USA.*
- Moghadam, H. S. and M. Helbich (2013).** "Spatiotemporal urbanization processes in the megacity of Mumbai, India: A Markov chains-cellular automata urban growth model." *Applied Geography* 40: 140-149.
- Monden, S. (2007).** "Vismigratie en het oplossen van vismigratieknelpunten." *Water Congres watersysteemkennis 2006-2007.*
- Morrow, J. E. (1980).** The freshwater fishes of Alaska, University of B.C., Animal Resources Ecology Library.

- Moustakas, A. and W. Silvert (2011).** "Spatial and temporal effects on the efficacy of marine protected areas: implications from an individual based model." *Stochastic Environmental Research and Risk Assessment* 25(3): 403-413.
- Mouton, A. (2008).** A critical analysis of performance criteria for the evaluation and optimization of fuzzy models for species distribution. Ghent, Belgium, Ghent University: 181.
- Mouton, A., D. Buysse, M. Stevens, T. Van den Neucker and J. Coeck (2011a).** "Evaluation of riparian habitat restoration in a lowland river." *River Research and Applications*.
- Mouton, A., B. De Baets and P. L. M. Goethals (2009a).** "Knowledge-based versus datadriven fuzzy habitat suitability models for river management." *Environmental Modelling and Software* 24: 982-993.
- Mouton, A., I. G. Jowett, P. L. M. Goethals and B. De Baets (2009a).** "Prevalence adjusted optimisation of a fuzzy habitat suitability model for aquatic invertebrate and fish species in New Zealand." *Ecological Informatics* 4: 215-225.
- Mouton, A., M. Schneider, P. Armin, G. Holzer, R. Müller, P. L. M. Goethals and N. De Pauw (2008a).** "Optimisation of a fuzzy physical habitat model for spawning European grayling (*Thymallus thymallus* L.) in the Aare river (Thun, Switzerland)." *Ecological Modelling* 215: 122-132.
- Mouton, A., M. Schneider, J. Depestele, P. L. M. Goethals and N. De Pauw (2007).** "Fish habitat modelling as a tool for river management." *Ecological Engineering* 29: 305-315.
- Mouton, A. M., J. D. Alcaraz-Hernandez, B. De Baets, P. L. M. Goethals and F. Martinez-Capel (2011b).** "Data-driven fuzzy habitat suitability models for brown trout in Spanish Mediterranean rivers." *Environmental Modelling & Software* 26(5): 615-622.
- Mouton, A. M., D. Buysse, M. Stevens, T. Van den Neucker and J. Coeck (2012a).** "Evaluation of Riparian Habitat Restoration in a Lowland River." *River Research and Applications* 28(7): 845-857.
- Mouton, A. M., B. De Baets and P. L. M. Goethals (2009b).** "Knowledge-based versus data-driven fuzzy habitat suitability models for river management." *Environmental Modelling & Software* 24(8): 982-993.
- Mouton, A. M., A. Dillen, T. Van den Neucker, D. Buysse, M. Stevens and J. Coeck (2012b).** "Impact of sampling efficiency on the performance of data-driven fish habitat models." *Ecological Modelling*.
- Mynett, A. and Q. W. Chen (2004).** "Cellular automata in ecological and ecohydraulics modelling." *Cellular Automata, Proceedings* 3305: 502-512.
- Nilsson, P. A., L. Jacobsen, S. Berg and C. Skov (2009).** "Environmental Conditions and Intraspecific Interference: Unexpected Effects of Turbidity on Pike (*Esox lucius*) Foraging." *Ethology* 115(1): 33-38.
- Northcote, T. G. (1978).** Migratory strategies and production in freshwater fish. Ecology of freshwater fish production. S. D. Gerking. Oxford, Blackwell Scientific Publications: 326-259.
- O'Callaghan, M. and G. N. G. Gordon (2008).** "An individual-based stochastic hazard model of eastern king prawn (*Melicertus plebejus*) migration with spatially and temporally varying fishing effort." *Ecological Modelling* 218(1-2): 73-94.
- Ovidio, M. and J. C. Philippart (2003).** Long range seasonal movements of northern pike (*Esox lucius* L.) in the barbel zone of the River Ourthe (River Meuse basin, Belgium). Fifth Conference on Fish Telemetry held in Europe, Ustica, Italy.
- Pauwels, I. S., G. Everaert and P. L. M. Goethals (2010).** "Integrated river assessment by coupling water quality and ecological assessment models." *Proceedings of the iEMSs Fifth Biennial Meeting : International Congress on Environmental Modelling and Software (2010)*: 1-9.

- Pauwels, I. S., P. L. M. Goethals, J. Coeck and A. M. Mouton (2014).** "Movement patterns of adult pike (*Esox Lucius* L.) in a Belgian lowland river." *Ecology of Freshwater Fish* 23: 373-382.
- Perez-Ocon, F., M. Rubino, A. M. Pozo and O. Rabaza (2013).** "Design of new traffic lights: Traffic safety and maintenance ease." *Engineering Structures* 57: 388-392.
- Perry, G. L. W. and N. R. Bond (2009).** "Spatially explicit modeling of habitat dynamics and fish population persistence in an intermittent lowland stream." *Ecological Applications* 19(3): 731-746.
- Perry, G. L. W. and N. J. Enright (2007).** "Contrasting outcomes of spatially implicit and spatially explicit models of vegetation dynamics in a forest-shrubland mosaic." *Ecological Modelling* 207: 327-338.
- Persson, L., A. Bertolo and A. M. De Roos (2006).** "Temporal stability in size distributions and growth rates of three *Esox lucius* L. populations. A result of cannibalism?" *Journal of Fish Biology* 69(2): 461-472.
- Petersen, J. H. and D. L. DeAngelis (2000).** "Dynamics of prey moving through a predator field: a model of migrating juvenile salmon." *Mathematical Biosciences* 165(2): 97-114.
- Pine, W. E., III, B. Healy, E. O. Smith, M. Trammell, D. Speas, R. Valdez, M. Yard, C. Walters, R. Ahrens, R. Vanhaverbeke, D. Stone and W. Wilson (2013).** "An Individual-Based Model for Population Viability Analysis of Humpback Chub in Grand Canyon." *North American Journal of Fisheries Management* 33(3): 626-641.
- Pola, N. B. (1985).** "NUMERICAL-SIMULATION OF FISH MIGRATIONS IN THE EASTERN BERING SEA." *Ecological Modelling* 29(1-4): 327-351.
- Prato, T. (2009).** "Adaptive management of natural systems using fuzzy logic." *Environmental Modelling & Software* 24(8): 940-944.
- Queiroz, N., N. E. Humphries, L. R. Noble, A. M. Santos and D. W. Sims (2010).** "Short-term movements and diving behaviour of satellite-tracked blue sharks *Prionace glauca* in the northeastern Atlantic Ocean." *Marine Ecology Progress Series* 406: 265-279.
- R Development Core Team (2008).** R: A language and environment for statistical computing. Vienna, Austria, R Foundation for Statistical Computing.
- Raat, A. J. P. (1988a).** Synopsis of biological data on the northern pike (*Esox lucius* Linnaeus, 1758), FAO Fisheries Synopsis, 30.
- Raat, A. J. P., Ed. (1988b).** Synopsis of biological data on the northern pike, *Esox lucius* (Linnaeus 1758). Organisator ter verbetering van de binnenvisserij, FAO of the United Nations, Rome, FAO Fisheries Synopsis.
- Radomski, P. and T. J. Goeman (2001).** "Consequences of human lakeshore development on emergent and floating-leaf vegetation abundance." *North American Journal of Fisheries Management* 21(1): 46-61.
- Railsback, S. F. and B. C. Harvey (2002).** "Analysis of habitat-selection rules using an individual-based model." *Ecology* 83(7): 1817-1830.
- Railsback, S. F., R. H. Lamberson, B. C. Harvey and W. E. Duffy (1999).** "Movement rules for individual-based models of stream fish." *Ecological Modelling* 123(2-3): 73-89.
- Robertson, M. P., M. H. Villet and A. R. Palmer (2004).** "A fuzzy classification technique for predicting species' distributions: applications using invasive alien plants and indigenous insects." *Diversity and Distributions* 10(5-6): 461-474.
- Rogers, K. B. and G. C. White (1990).** Analysis of movement and habitat use from telemetry data. Analysis of wildlife radio-tracking data. G. C. White and R. A. Garrott, Academic Press, 1990: 625-676.
- Rogers, P. J., C. Huveneers, S. D. Goldsworthy, J. G. Mitchell and L. Seuront (2013).** "Broad-scale movements and pelagic habitat of the dusky shark *Carcharhinus obscurus* off

- Southern Australia determined using pop-up satellite archival tags." *Fisheries Oceanography* 22(2): 102-112.
- Rohde, K. (2005).** "Cellular automata and ecology." *Oikos* 110(1): 103-207.
- Rose, K. A., J. Cowan, K. O. Winemiller, R. A. Myers and R. Hilborn (2001).** "Compensatory density dependence in fish populations importance controversy understanding and prognoses." *Fish and Fisheries* 2: 293-327.
- Ruxton, G. D. and L. A. Saravia (1998).** "The need for biological realism in the updating of cellular automata models." *Ecological Modelling* 107(2-3): 105-112.
- Sakabe, R. and J. M. Lyle (2010).** "The influence of tidal cycles and freshwater inflow on the distribution and movement of an estuarine resident fish *Acanthopagrus butcheri*." *Journal of Fish Biology* 77(3): 643-660.
- Sammons, S. M., C. G. Scalet and R. M. Neumann (2011).** "Seasonal and size-related changes in the diet of Northern pike from a shallow prairie lake." *Journal of Freshwater Ecology* 9(4): 321-329.
- Schabetsberger, R., F. Okland, K. Aarestrup, D. Kalfatak, U. Sichrowsky, M. Tambets, G. Dall'Olmo, R. Kaiser and P. I. Miller (2013).** "Oceanic migration behaviour of tropical Pacific eels from Vanuatu." *Marine Ecology Progress Series* 475: 177-190.
- Scott, W. B. and E. J. Crossman (1973).** Freshwater fishes of Canada. Ottawa, Fisheries Research Board Canada.
- Shannon, C. E. (1948).** "A mathematical theory of communication." *Bell System Technical Journal* 27: 379-423.
- Skov, C. and S. Berg (1999).** "Utilization of natural and artificial habitats by YOY pike in a biomanipulated lake." *Hydrobiologia* 408: 115-122.
- Skov, C., S. Berg, L. Jacobsen and N. Jepsen (2002).** "Habitat use and foraging success of 0+pike (*Esox lucius* L.) in experimental ponds related to prey fish, water transparency and light intensity." *Ecology of Freshwater Fish* 11(2): 65-73.
- Skov, C., L. Jacobsen and S. Berg (2003a).** "Post-stocking survival of 0+year pike in ponds as a function of water transparency, habitat complexity, prey availability and size heterogeneity." *Journal of Fish Biology* 62(2): 311-322.
- Skov, C. and A. Koed (2004).** "Habitat use of 0+year pike in experimental ponds in relation to cannibalism, zooplankton, water transparency and habitat complexity." *Journal of Fish Biology* 64(2): 448-459.
- Skov, C., O. Lousdal, P. H. Johansen and S. Berg (2003b).** "Piscivory of 0+pike (*Esox lucius* L.) in a small eutrophic lake and its implication for biomanipulation." *Hydrobiologia* 506(1-3): 481-487.
- Smith, B. M., J. M. Farrel, H. B. Underwood and S. J. Smith (2007).** "Year-Class Formation of Upper St. Lawrence River Northern Pike." *North American Journal of Fisheries Management* 27: 481-491.
- Smith, I. P., D. J. Booker and N. C. Wells (2009).** "Bioenergetic modelling of the marine phase of Atlantic salmon (*Salmo salar* L.)." *Marine Environmental Research* 67(4-5): 246-258.
- Soupir, C. A., M. L. Brown and L. W. Kallemeyn (2000).** "Trophic ecology of largemouth bass and northern pike in allopatric and sympatric assemblages in northern boreal lakes." *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 78(10): 1759-1766.
- Spens, J., G. Englund and H. Lundqvist (2007).** "Network connectivity and dispersal barriers: using geographical information system (GIS) tools to predict landscape scale distribution of a key predator (*Esox lucius*) among lakes." *Journal of Applied Ecology* 44(6): 1127-1137.
- Spillman, C. J. (1961).** Faune de France: Poissons d'eau douce. Paris, Fédération Française des Sociétés Naturelles, Tome 65.

- Stefansson, G. and A. A. Rosenberg (2006).** "Designing marine protected areas for migrating fish stocks." *Journal of Fish Biology* 69(Supplement C): 66-78.
- Stocker, S. (1999).** "Models for tuna school formation." *Mathematical Biosciences* 156(1-2): 167-190.
- Swihart, R. K. and N. A. Slade (1985).** "Testing for Independence of Observations in Animal Movements." *Ecology* 66(4): 1176-1184.
- Tao, S., Z. Linghan, C. Wangli, T. Xianxiu and Q. Qianqing (2013).** "Mountains Forest Fire Spread Simulator Based on Geo-Cellular Automaton Combined With Wang Zhengfei Velocity Model." *IEEE Journal of Selected Topics In Applied Earth Observations And Remote Sensing* 6(4): 1971-1987.
- Thatcher, J. (1964).** Universality in the von Neumann cellular model. Technical report 03105-30-T. Michigan, University of Michigan.
- Toffoli, T. (1984).** "Cellular Automata as an Alternative to (Rather Than an Approximation of) Differential-Equations in Modeling Physics." *Physica D* 10(1-2): 117-127.
- Treasurer, J. W., R. Owen and E. Bowers (1992).** "The Population-Dynamics of Pike, *Esox-Lucius*, and Perch, *Perca-Fluviatilis*, in a Simple Predator-Prey System." *Environmental Biology of Fishes* 34(1): 65-78.
- Tyler, J. A. and K. A. Rose (1997).** "Effects of individual habitat selection in a heterogeneous environment on fish cohort survivorship: A modelling analysis." *Journal of Animal Ecology* 66(1): 122-136.
- U.S. Fish and Wildlife Service (1981).** Standards for the development of habitat suitability index models, U.S. Department of International Affairs, Fish and Wildlife Service. ESM 103.
- Uchmanski, J., D. Aikman, T. Wyszomirski and V. Grimm (1999).** "Individual-based modelling in ecology - Preface." *Ecological Modelling* 115(2-3): 109-110.
- Vabo, R. and L. Nottestad (1997).** "An individual based model of fish school reactions: predicting antipredator behaviour as observed in nature." *Fisheries Oceanography* 6(3): 155-171.
- Vandelannoote, A., R. Yseboodt, B. Bruylants, R. Verheyen, J. Coeck, J. Maes, C. Belpaire, G. Van Thuyne, B. Denayer, J. Beyens, D. De Charleroy and P. Vandenabeele, Eds. (1998).** Atlas van de Vlaamse beek- en riviervissen, v.z.w. WEL.
- Vandenabeele, P., C. Belpaire, B. Denayer, J. Beyens, R. Yseboodt, L. Samsoen, G. Van Thuyne and J. Maes (1998).** "De visstand en de bevissing van de Vlaamse binnenwateren." *Water* 100: 14.
- Vehanen, T., P. Hyvarinen, K. Johansson and T. Laaksonen (2006).** "Patterns of movement of adult northern pike (*Esox lucius* L.) in a regulated river." *Ecology of Freshwater Fish* 15(2): 154-160.
- Venturelli, P. A. and W. M. Tonn (2006).** "Diet and growth of northern pike in the absence of prey fishes: Initial consequences for persisting in disturbance-prone lakes." *Transactions of the American Fisheries Society* 135(6): 1512-1522.
- Venturini, A. (2011).** "Time series outlier detection: a new non parametric methodology (washer)." *Statistica* 1: 329-344.
- Verreycken, H., G. Van Thuyne, C. Belpaire, J. Breine, D. Buysse, J. Coeck, A. Mouton, M. Stevens, T. Van den Neucker, L. De Bruyn and D. Maes (2012).** De IUCN rode lijst van zoetwatervissen in Vlaanderen. Brussel, Instituut voor Natuur en Bosonderzoek. Rapporten van het Instituut voor Natuur- en Bosonderzoek (23).
- Vicsek, T., A. Czirok, E. Benjacob, I. Cohen and O. Shochet (1995).** "Novel Type of Phase-Transition in a System of Self-Driven Particles." *Physical Review Letters* 75(6): 1226-1229.

- Vicsek, T., A. Czirok, I. J. Farkas and D. Helbing (1999).** "Application of statistical mechanics to collective motion in biology." *Physica a-Statistical Mechanics and Its Applications* 274(1-2): 182-189.
- Vilizzi, L., G. H. Copp and J. M. Roussel (2004).** "Assessing variation in suitability curves and electivity profiles in temporal studies of fish habitat use." *River Research and Applications* 20(5): 605-618.
- VMM (2012).** MIRA indicator rapport 2012, Vlaamse Milieumaatschappij (VMM).
- von Neumann, J. (1966).** Theory of self-reproducing automata. Urbana, University of Illinois Press.
- Walsh, C. T., I. V. Reinfelds, R. J. West, C. A. Gray and D. E. van der Meulen (2012).** "Distribution and Movement of Catadromous Fish: Design and Implementation of a Freshwater-Estuarine Acoustic Telemetry Array." *Advances in Fish Tagging and Marking Technology* 76: 251-264.
- Wang, Y., H. Wei and M. J. Kishi (2013).** "Coupling of an individual-based model of anchovy with lower trophic level and hydrodynamic models." *Journal of Ocean University of China* 12(1): 45-52.
- Watkins, K. S. and K. A. Rose (2013).** "Evaluating the performance of individual-based animal movement models in novel environments." *Ecological Modelling* 250: 214-234.
- Webb, P. W. and J. M. Skadsen (1980).** "Strike Tactics of Esox." *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 58(8): 1462-1469.
- Weber, L. J., R. A. Goodwin, S. Li, J. M. Nestler and J. J. Anderson (2006).** "Application of an Eulerian-Lagrangian-Agent method (ELAM) to rank alternative designs of a juvenile fish passage facility." *Journal of Hydroinformatics* 8(4): 271-295.
- Werner, F. E., J. A. Quinlan, R. G. Lough and D. R. Lynch (2001).** "Spatially-explicit individual based modeling of marine populations: a review of the advances in the 1990s." *Sarsia* 86(6): 411-421.
- Willems, W., P. L. M. Goethals, D. Van Den Eynde, G. Van Hoey, V. Van Lancker, E. Verfaillie, M. Vincx and S. Degraer (2008).** "Where is the worm? Predictive modelling of the habitat preference of the tube building polychaete *Lanice conchilega*." *Ecological Modelling* 212: 74-79.
- Williams, J., T. Speed and W. Forrest (1999).** "Comment: transferability of habitat suitability criteria." *North American Journal of Fisheries Management* 19(2): 623-625.
- Willis, J. (2011).** "Modelling swimming aquatic animals in hydrodynamic models." *Ecological Modelling* 222(23-24): 3869-3887.
- Wolfram, S. (1983).** "Statistical mechanics of cellular automata." *Reviews of Modern Physics* 55(3): 601-644.
- Wolfram, S. (1986).** Theory and applications of cellular automata. Singapore, World Scientific.
- Wolfram, S. (1994).** Cellular automata and complexity, Addison-Wesley Reading, MA.
- Wood, S. (2006).** Generalized additive mixed models: an introduction with R. Boca Raton, Chapman & Hall/CRC Press.
- Xie, Y., A. Ma and H. Wang (2010).** "Lanzhou Urban Growth Prediction Based on Cellular Automata." *2010 18th International Conference on Geoinformatics*.
- Xu, X., F. Zhang, J. Zhang and Ieee (2006).** Modelling the Impacts of Different Policy Scenarios on Urban Growth in Lanzhou with Remote Sensing and Cellular Automata.
- Yassemi, S., S. Dragicevic and M. Schmidt (2008).** "Design and implementation of an integrated GIS-based cellular automata model to characterize forest fire behaviour." *Ecological Modelling* 210: 71-84.

- Yemane, D., Y. Shin and J. G. Field (2008).** "Exploring the effects of marine protected areas on the dynamics of fish communities in the southern Benguela: an individual-based modeling approach." *Ices Journal of Marine Science* 66: 378-387.
- Yemane, D., Y. J. Shin and J. G. Field (2009).** "Exploring the effect of Marine Protected Areas on the dynamics of fish communities in the southern Benguela: an individual-based modelling approach." *Ices Journal of Marine Science* 66(2): 378-387.
- Zadeh, L. A. (1965).** "Fuzzy Sets." *Information and Control* 8(3): 338-&.
- Zeng, J., Y. Xue, Y. Qian, W. Li, D. Xu, X. Guang and M. Wang (2014).** "Study on the effect of redundant time on the operation of mixed passenger and freight traffic system using cellular automata model." *Measurement* 47: 724-733.
- Ziv, G., E. Baran, S. Nam, I. Rodriguez-Iturbe and S. A. Levin (2012).** "Trading-off fish biodiversity, food security, and hydropower in the Mekong River Basin." *Proceedings of the National Academy of Sciences of the United States of America* 109(15): 5609-5614.
- Zorn, T. G., P. W. Seelbach and E. S. Rutherford (2012).** "A Regional-Scale Habitat Suitability Model to Assess the Effects of Flow Reduction on Fish Assemblages in Michigan Streams." *Journal of the American Water Resources Association* 48(5): 871-895.
- Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev and G. M. Smith (2009).** Mixed effects models and extensions in ecology with R. New York, Springer.

Summary

Last decades, substantial efforts are made in Flanders (Belgium) to enhance the ecological river quality. These efforts have largely and successfully concentrated on improvement of the chemical water quality. Notwithstanding, the biological quality is still far from the intended standard and many aquatic species have not regained a healthy status. The greatest cause so far beside the moderate water quality, is a lagging habitat quality by habitat deterioration and fragmentation. Aquatic species that are mostly affected by habitat degradation and fragmentation are definitely fish and specifically migratory fish. The habitats that migratory fish use to feed, rest, hide and reproduce may be very dispersed making free migration between these habitats essential to survive.

The success of management plans to restore river habitats and enhance the accessibility requires good knowledge on the status of the aquatic system, the main bottlenecks and the ecology of the target species. Integrating this knowledge in models can help to quantitatively predict the impact of specific measures and may help to better understand the habitat requirements and spatial dynamics of the fish. Habitat suitability and species distribution models are helpful tools in understanding the suitability of local, critical habitat variables such as water depth, flow velocity and vegetation characteristics and have thoroughly been studied during past decades. However, these models do not allow to model population viability constraints by wider, large scale variables, such as migratory access. Two modelling techniques that may account for these factors are IBMs and CAs.

The aim of this PhD was to support river management with knowledge on northern pike *Esox lucius* L. ecology by the development of a spatially explicit modelling method that allows to assess the effect of river restoration measures by simulation of adult pike migration. Therefore, the applicability to simulate pike migration of the CA and IBM modelling techniques was evaluated and field data on adult pike in a lowland river were analysed to evaluate pike's movement and migration dynamics and its habitat use and preference. The field data were collected by radio telemetry in the river Yser and different methods were assessed and applied to study adult pike's migration dynamics, habitat use and preference. The results were further evaluated by a rule-based habitat suitability model for adult pike in a lowland river that was developed based on expert knowledge and the adult pike field data collected during this study.

The results of the IBM and CA-based model evaluations indicated that simulation of individual pike migration in a reliable and detailed way is possible using an IBM. A major advantage of the model is that it could be further adapted for pike or could be easily adapted

to another fish species by further fine tuning of the model parameters. Beside it enables the simulation of individual fish, which might be of greater importance than previously thought. However, the model is complex, which might reduce the user friendliness and transparency towards river managers. In contrast, the CA-based model is simpler and more transparent, but an evaluation of its applicability indicated sensitivity of the model for model parameters such as the density of the pike and the resolution of the grid in which simulations are performed and which represents the river area. Although the sensitivity was lower after adaptations on the definition of the environmental suitability and the neighbourhood, the model still did not properly simulate adult pike migration at densities of one pike per grid cell. It is suggested that further research on the transition rules applied in the CA-based model may potentially solve the problems encountered. However, the results indicate that the coupling of ecological processes and environmental variables on different spatial scales is much more difficult than expected before the start of this research.

The statistical analyses of the adult pike radio telemetry data revealed that four environmental variables significantly affected pike migration, ranging from the location where pike were observed (strongest effect), over water temperature and flow to the diel water temperature change (weakest effect). The results on the relation between water temperature and migration in our study suggested that 9 to 10 °C might be a threshold level for migration in this region. Based on our results river managers could consider the impact of water temperature on pike migration to facilitate the accessibility of small tributaries and spawning grounds, e.g. by opening valves at water temperatures between 0 and 12 °C. The apparent inhibition of pike migration at high flows suggests that pike could benefit from the buffering of peak flows, e.g. by restoring floodplains and increasing lateral connectivity.

The results of the study on the habitat use and preference of adult pike for the riparian habitats at the macro- and meso-scale indicated substantial individual differences and generally underpin the previously suggested versatile habitat use of adult pike. The latter result was also supported by the rule base of the habitat suitability model developed in this thesis. The analysis of the habitat use and preference could reveal the importance of small tributaries upstream in the river Yser and suggests a rather low benefit of adult pike from artificial spawning grounds. The results further indicated the importance of habitat heterogeneity both at the macro- and meso-scale, which could be conserved and rehabilitated on different levels. River managers could focus on the lateral connectivity between the main river and its tributaries and side arms to conserve and optimize the heterogeneity at the macro-scale and could protect and rehabilitate riparian habitats that enable growth of emergent reed and of woody vegetation like trees and shrubs on the banks. Despite river restoration efforts, our findings underline the value of least impacted, (semi)natural habitats in an anthropogenic river system.

This thesis contributed to both the spatially explicit simulation of pike migration, knowledge on pike ecology with direct suggestions for river management and the methodology on properly analysing telemetry data from riverine fish; by providing insight into the applicability of the IBM and CA-modelling techniques and the application and assessment of different telemetry data analysis techniques.

Samenvatting

De laatste decennia zijn aanzienlijke inspanningen geleverd in Vlaanderen (België) om de ecologische kwaliteit in onze rivieren te verbeteren. Deze pogingen waren en zijn, grotendeels met succes, gericht op een verbetering van de chemische waterkwaliteit. Niettegenstaande, is de biologische kwaliteit nog steeds ver van de beoogde standaard en bijgevolg bereiken verschillende groepen van aquatische organismen geen gezonde ecologische kwaliteit. De grootste oorzaak naast de matige kwaliteit van het water, is tot dusver een ondermaatse kwaliteit van de leefomgeving door habitatverlies, habitatdegradatie en versnippering. Aquatische soorten die hier het meest door worden beïnvloed zijn vissen en specifiek trekvis. De habitats die trekvis gebruiken om zich te voeden, om te rusten, zich te verstoppen en zich voort te planten zijn doorgaans ruimtelijk verspreid, wat vrije migratie tussen deze habitats essentieel maakt om te overleven.

Het succes van beheersplannen voor het herstel en de verbetering van de habitatkwaliteit en de bereikbaarheid vereist goede kennis over de status van het aquatisch systeem, de belangrijkste knelpunten en de ecologie van de doelsoorten. Integratie van deze kennis in modellen kan helpen om de effecten van specifieke maatregelen kwantitatief te voorspellen en kan helpen om het leefgebied, de habitat eisen en ruimtelijke dynamiek van verschillende vissoorten beter te begrijpen. Habitat geschiktheids- en verspreidingsmodellen zijn handige hulpmiddelen bij het begrijpen van de geschiktheid van de plaatselijke leefgebieden, en kritische variabelen zoals de waterdiepte, stroomsnelheid en vegetatie. Echter, deze modellen laten niet toe om grootschaligere variabelen in rekening te brengen, zoals migratieprocessen. Twee modelleringstechnieken die echt ruimtelijk expliciet zijn en daardoor mogelijk in staat zijn om deze factoren in rekening te brengen zijn individueel-gebaseerde modellen (IBM's) en cellulaire automaten (CA's).

Het doel van dit doctoraatsonderzoek is het rivierbeheer te ondersteunen met kennis over de ecologie van snoek *Esox lucius* L. door de evaluatie van ruimtelijk expliciete en dynamische modellerende technieken die mogelijk maken om effecten van mogelijke rivier herstel maatregelen te beoordelen via de simulatie van migratie van volwassen snoek in een rivier. Daarom werd de toepasbaarheid van de CA en IBM modelleringstechnieken voor het simuleren van snoek migratie geëvalueerd en werden veldgegevens van snoek geanalyseerd om zijn bewegings- en migratiedynamiek en zijn habitatgebruik en voorkeur te evalueren. De veldgegevens werden binnen dit onderzoek verzameld met behulp van radio telemetrie in de IJzer (West-Vlaanderen, België). Gedurende een periode van 6 maanden werden enkele studiedieren zeer intensief opgevolgd en werd dagelijks tot drie-dagelijks hun positie bepaald.

in een gebied van meer dan 60 km toegankelijke waterlopen. Verschillende methoden werden beoordeeld en toegepast om op basis van deze data het migratiegedrag van de volwassen snoek en het gebruik en de voorkeur voor zijn leefgebied te bestuderen. De resultaten werden verder geëvalueerd via de ontwikkeling van een habitatgeschiktheidsmodel voor volwassen snoek in een laagland rivier dat werd ontwikkeld op basis van een combinatie van vakkennis en veldgegevens. Behalve het gebruik van de veldgegevens voor modelontwikkeling, werden de gegevens dus ook rechtstreeks gebruikt om ondersteuning te bieden aan het rivierbeheer onder de vorm van kennis over het migratiegedrag en habitatgebruik van de adulte snoek.

De resultaten van de IBM en CA-gebaseerde model evaluaties geven aan dat simulatie van afzonderlijke individuen op een betrouwbare en gedetailleerde wijze mogelijk is met behulp van een IBM. Een groot voordeel van het model is dat via het optimaliseren van de verschillende modelparameters die de simulatie van migratie sturen, het model nog meer betrouwbaar gemaakt kan worden voor snoek en zelfs gemakkelijk kan worden aangepast zodat het ook op andere vissoorten van toepassing is. De grote complexiteit van het model wordt echter wel als een mogelijks nadeel gezien, omdat dit de gebruiksvriendelijkheid en begrijpbaarheid van het model eventueel kan verminderen. In tegenstelling tot de IBM's zijn de CA-gebaseerde model wel veel eenvoudiger en transparanter om te begrijpen, maar ook om te implementeren eens de juiste transitie regels en model instellingen ontdekt zijn. De evaluatie toonde echter wel aan dat het model, zoals het momenteel opgebouwd is, zeer gevoelig is aan model eigenschappen zoals de snoekdensiteit in het studiegebied versus de resolutie van het raster dat het studiegebied voorstelt. Zelfs na aanpassing van de definitie van de habitatgeschiktheid in iedere cel van het raster en de definitie van de buurt die mee de migratie bepaalt is het model nog steeds niet in staat om migratie te simuleren wanneer de snoek densiteit gereduceerd is tot 1 snoek per raster cel. Verder onderzoek naar de transitieregels van het model dringt zich op om dit probleem op te lossen.

De statistische analyses van de migratiedynamiek van snoek op basis van de veldgegevens toonden aan dat migratie significant beïnvloed werd door vier omgevingsvariabelen, variërend van de locatie waar snoek werd waargenomen (sterkste effect), over water temperatuur en het debiet naar de dagelijkse water temperatuursveranderingen (zwakste effect). De resultaten suggereerde specifiek dat 9 tot 10 ° C een drempelwaarde voor migratie zou kunnen zijn voor snoeken in deze regio. Deze resultaten suggereren een positief effect van het toegankelijk houden of maken van zijriviertjes en andere potentiële paaigebieden voor snoek gedurende de paaiperiode bij watertemperaturen tussen 0 en 12°C.

De schijnbare inhibitie van migratie bij hoge debieten suggereert dat snoek zou kunnen profiteren van de buffering van piekafvoeren, specifiek tijdens de paaiperiode, bijv. door het herstel van overstromingsgebieden en een verhoogde laterale connectiviteit.

De resultaten van de studie naar het gebruik en de preferentie van snoek voor oever habitats op macro- en meso-schaal gaf aan dat het gebruik en de preferentie aanzienlijk kan verschillen tussen individuen en dat in het algemeen de grote volwassen snoeken weinig kieskeurig zijn naar hun habitat toe en verschillende types habitat gebruiken. Het laatste werd ook ondersteund door de regelbank die resulteerde uit het habitatgeschiktheidsmodel dat ontwikkeld werd tijdens deze studie. De analyse van het habitatgebruik en de preferentie wees verder op het belang van kleine zijrivieren stroomopwaarts in de IJzer en suggereren een eerder klein tot onbestaand voordeel van kunstmatig aangelegde paaiplaatsen voor paaiende snoek. De resultaten wezen tot slot op het belang van de habitat diversiteit, zowel op macro- als meso-schaal en we gaven aan hoe deze op verschillend niveaus behouden of hersteld kan worden. Rivierbeheerders zouden zich kunnen richten op de laterale connectiviteit tussen de belangrijkste rivier en haar zijrivieren en zijarmen om zo de habitat diversiteit op macro-schaal te behouden of zelfs te bevorderen en zouden oever habitats die de groei van rietige en houtige vegetatie toelaten kunnen behouden. Ondanks de reeds geleverde inspanningen naar

oeverherstel toe, onderstrepen onze bevindingen de waarde van de minst aangetaste half-natuurlijke habitats in een antropogeen riviersysteem.

Dit proefschrift heeft zowel aan de ruimtelijke expliciete simulatie van snoek migratie bijgedragen, als aan de ecologie van snoek en het beheer ervan, via enerzijds directe aanbevelingen en anderzijds via het evalueren van verschillende methoden die een correcte analyse van telemetriegegevens toelaten.

Curriculum Vitae

Personalia

Naam	Ine Pauwels
Geslacht	Vrouwelijk
Nationaliteit	Belg
Geboortedatum	01/04/1986, 28 jaar
Geboorteplaats	Bornem, België
Burgerlijke stand	Wettelijk samenwonend
e-mail	Ine.Pauwels@ugent.be

Opleiding

1999 – 2004	Secundair onderwijs, Latijn-Wiskunde (6u), Onze Lieve Vrouw Presentatie Bornem
2004 – 2007	Bachelor in de biologie, onderscheiding optie Ecologie, Faculteit Wetenschappen, Universiteit Gent Thesis: 'Rekolonisatie van slikken platen in de Westerschelde (België) door macrobenthos.' Promotoren: Dr. Steven Degraer en Dr. Carl Van Colen
2007 – 2009	Master in de biologie, grote onderscheiding optie Ecologie en Biodiversiteit, Faculteit Wetenschappen, Universiteit Gent Thesis: 'Lange-termijn verschuivingen in de fytoplanktongemeenschappen van de Zeeschelde, en de invloed van begrazing door zooplankton en de amoebe Asterocaelum.' Promotoren: Prof. Dr. Wim Vyverman en Prof. Dr. Koen Sabbe
2010 – 2014	Doctoraatsopleiding in de Toegepaste Biologische Wetenschappen, Universiteit Gent, Faculteit Bio-ingenieurswetenschappen

Loopbaanoverzicht - werkervaring

2009 – 2010	Wetenschappelijk medewerker, Labo voor Milieutoxicologie en Aquatische Ecologie, Faculteit Bio-ingenieurswetenschappen, Universiteit Gent
2010-2013	IWT-bursaai, Labo voor Milieutoxicologie en Aquatische Ecologie, Faculteit Bio-ingenieurswetenschappen, Universiteit Gent
2013-2014	Wetenschappelijk medewerker, Labo voor Milieutoxicologie en Aquatische Ecologie, Faculteit Bio-ingenieurswetenschappen, Universiteit Gent
2014-heden	Onderzoeker Instituut voor Natuur- en Bosonderzoek (INBO), Onderzoeksgroep Aquatisch Beheer, Brussel.

Wetenschappelijke activiteiten

Publicaties

A1 publicaties, opgenomen in één van de ISI Web of Science databanken (chronologisch; oudste eerst)

Everaert, G., Pauwels, I.S., Boets, P., Buysschaert, F., Goethals, P.L.M. 2013. Development and assessment of ecological models in the context of the European Water Framework Directive: key issues for trainers in data-driven modelling approaches. *Ecological Informatics* 17: 111-116.

Everaert, G., Pauwels, I.S., Boets, P., Verduin, E., de la Haye, M.A.A., Blom, C., Goethals, P.L.M. 2013. Model-based evaluation of ecological bank design and management in the scope of the European Water Framework Directive. *Ecological Engineering* 53: 144-152.

Pauwels, I.S., Mouton, A.M., Baetens, J.M., Van Nieuland, S., De Baets, B. & Goethals, P.L.M. 2013. Modelling a pike (*Esox lucius*) population in a lowland river using a cellular automaton. *Ecological Informatics* 17: 46-57.

Baetens, J.M., Van Nieuland, S., Pauwels, I.S., De Baets, B., Mouton, A.M., Goethals, P.L.M. 2013. An individual-based model for the migration of pike (*Esox lucius*) in the river Yser, Belgium. *Ecological Modelling* 258: 40-52.

Pauwels, I.S., Goethals, P.L.M., Coeck, J., Mouton, A.M. 2014. Movement patterns of adult pike (*Esox lucius* L.) in a Belgian lowland river. *Ecology of Freshwater Fish* 23: 373-382.

Pauwels, I.S., Goethals, P.L.M., Coeck, J., Mouton, A.M. submitted. Habitat use of adult pike (*Esox lucius* L.) in a lowland river. *Hydrobiologia*.

Boets, P., Pauwels I.S., Lock K., Goethals P.L.M. 2013. Using an integrated modelling approach for risk assessment of the 'killer shrimp' *Dikerogammarus villosus*. *River Research and Applications* 30: 403-412.

Holguin-Gonzalez Javier E., Boets Pieter, Everaert Gert, Pauwels Ine S., Lock Koen, Gobeyn Sacha, Benedetti Lorenzo, Amerlinck Youri, Nopens Ingmar, Goethals Peter L.M. in press. Development and assessment of an integrated ecological modelling framework for decision support in water management. *Water Resources Management*.

A4 publicaties, niet peer-reviewed (chronologisch; oudste eerst)

Everaert, G., Pauwels, I.S., Goethals, P.L.M. 2010. Modellen voorspellen waterkwaliteit Vlaamse rivieren. *Aquarama. Vakblad voor Watertechnologie* 13(49): p.89-90.

Everaert, G., Pauwels, I.S., Goethals, P.L.M. 2011. Ecological river quality modelling supports Belgium's implementation of the European Water Framework Directive. *Water* 21 13(3): 56.

Pauwels, I.S., Mouton, A.M., Goethals, P.L.M. 2011. Supporting river management with a spatially explicit, dynamic model for pike populations. *Newsletter of the IWA specialist group on watershed and river basin management*, pp.27.

'Snoekmonitoring in de IJzer', De Vislijn, editie 2012, pp.17.

C1 publicaties, opgenomen in proceedings van internationale wetenschappelijke congressen (volledige artikels met uitsluiting van abstracts)

Everaert, G., Pauwels, I.S., Goethals, P.L.M. 2010. Development of data-driven models for the assessment of macroinvertebrates of rivers in Flanders. In: Swayne, D.A., Yang, W., Voinov, A.A., Rizzoli, A., Filatova, T. (Eds.), *Proceedings of the 5th biennial conference: "Modelling for environment's sake"*. International Environmental Modelling and Software Society, 5-8 July 2010, Ottawa, Canada, p.1984-1956.

Pauwels, I.S., Everaert, G., Goethals, P.L.M. 2010. Integrated river assessment by coupling water quality and ecological assessment models. In: Swayne, D.A., Yang, W., Voinov, A.A., Rizzoli, A., Filatova, T. (Eds.), *Proceedings of the 5th biennial conference: "Modelling for environment's sake"*. International Environmental Modelling and Software Society, 5-8 July 2010, Ottawa, Canada, p.876-884.

Van Nieuland, S., Baetens, J.M., Pauwels, I.S., Mouton, A.M., De Baets, B., Goethals, P.L.M. 2012. A spatially explicit migration model for pike. In: Sirakoulis, G.S., Bandini, S. (Eds.), *Proceedings of the 10th international conference on cellular automata for research and industry, ACRI, 24-27 September 2012, Santorini Island, Greece: Cellular Automata: Lecture notes in computer science* 7495: 763-767.

Presentaties

Internationale congressen, symposia en lezingen waarop een actieve bijdrage werd geleverd

Presentaties als spreker

Pauwels, I.S., Baetens, J.M., De Baets, B., Mouton, A.M., Goethals, P.L.M. A concept study for modelling a pike (*Esox lucius* L.) population using a cellular automaton. Gepresenteerd op het 7^e Internationale Congres van 'The Ecological Informatics Society', 13-16 december 2010, Gent, België.

Pauwels, I.S., Mouton, A.M., Goethals, P.L.M. Development of a spatially explicit and dynamic model for pike (*Esox lucius* L.) populations in rivers to support river management. Gepresenteerd op 'The Summerschool of Moving Objects and Knowledge Discovery', 22-26 augustus 2011, Gent, België.

Pauwels, I.S., Baetens, J.M., De Baets, B., Mouton, A.M., Goethals, P.L.M. Application of cellular automata to model population dynamics and migration of pike (*Esox lucius* L.) to support river management. Gepresenteerd op het 7^e Internationale Congres van 'Ecological Modelling', 30 mei - 2 juni 2011, Riva del Garda, Italië.

Pauwels, I.S., Mouton, A.M., Goethals, P.L.M. Integrating telemetry data and expert knowledge in a spatial-temporal model for pike (*Esox lucius*) in a lowland river. Gepresenteerd op het 8^e Internationale Congres van 'the Ecological Informatics Society', 3-7 december 2012, Brasilia, Brazilië.

Pauwels, I.S., Goethals, P.L.M., Coeck, J., Mouton, A.M. Integrating telemetry data and expert knowledge in a habitat suitability model for pike (*Esox lucius*) in a lowland river. Gepresenteerd op het 19^e tweejaarlijkse congres van 'The International Society on Ecological Modeling', 28-31 oktober 2013, Toulouse, Frankrijk.

Pauwels, I.S., Goethals, P.L.M., Coeck, J., Mouton, A.M. Evaluating the effect of river modifications on adult Northern pike with a spatially explicit habitat model. Gepresenteerd op het 10^e international congress van "Ecohydraulics", 23-27 juni 2014, Trondheim, Noorwegen.

Presentaties als co-auteur (spreker onderlijnd)

Pauwels, I.S., Everaert, G., Goethals, P.L.M. Integrated river assessment by coupling water quality and ecological assessment models. Gepresenteerd op het Internationale Congres van 'Environmental Modelling and Software': Modelling for environment's sake, 5-8 juli 2010, Ottawa, Canada.

Goethals, P.L.M., Zarkami, R., Pauwels, I.S., Boets, P., Lock, K., Mouton, A.M. Habitat suitability modelling for Master of Science students: case of pike modelling in Flanders. Gepresenteerd op het 7^e Internationale Congres van 'The Ecological Informatics Society', 13-16 december 2010, Gent, België.

Van Nieueland, S., Pauwels, I.S., Mouton, A.M., Goethals, P.L.M. Construction of a qualitative foodweb based dynamic habitat suitability model to describe pike populations in rivers. Gepresenteerd op het 7^e Internationale Congres van 'The Ecological Informatics Society', 13-16 december 2010, Gent, België.

Everaert, G., Pauwels, I.S., Verduin, E., de la Haye, M.A.A., Blom, C., Goethals, P.L.M. Development of datadriven models to analyze relations between ecologically sound bank quality and biological communities. Gepresenteerd op het 7^e Internationale Congres van 'The Ecological Informatics Society', 13-16 december 2010, Gent, België.

Zarkami, R., Pauwels, I.S., Everaert, G., Mouton, A., Goethals, P.L.M. Comparison of data mining methods for pike (*Esox lucius* L.) habitat suitability modelling in rivers. Gepresenteerd op het 7e Internationale Congres van 'The Ecological Informatics Society', 13-16 december 2010, Gent, België.

Everaert, G., Pauwels, I.S., Verduin, E., de la Hay, M.A.A., Blom, C., Goethals, P.L.M. Assessment of ecologically sound banks: model-based selection of key issues for design and management practices. Gepresenteerd op het 7e Internationale Congres van 'Ecological Modelling', 30 mei - 2 juni 2011, Riva del Garda, Italië.

Boets P., Pauwels I., Lock K., Goethals P.L.M. Using external model coupling for risk assessment of the 'killer shrimp' *Dikerogammarus villosus* in Flanders (Belgium). Gepresenteerd op het 8^e Internationale Congres van 'the Ecological Informatics Society', 3-7 december 2012, Brasilia, Brazilië.

Poster presentaties

Pauwels, I.S., Everaert, G., Goethals, P.L.M. Integrated River assessment by coupling water quality and ecological assessment models. Gepresenteerd op de Jaarlijkse Nederlandse Ecologie Meeting, 9-10 februari 2010, Lunteren, Nederland.

Everaert, G., Pauwels, I.S., Schneiders, A., Breine, J., Gabriels, W., D'heygere, T., Goethals, P.L.M. Added value of multi-community cascade models to analyse the relation between water quality conditions and ecological status of rivers. Gepresenteerd op de Jaarlijkse Nederlandse Ecologie Meeting, 9-10 februari 2010, Lunteren, Nederland.

Nationale congressen, symposia en lezingen waarop een actieve bijdrage werd geleverd

Presentaties als spreker

Pauwels, I.S., Coeck, J., Goethals, P.L.M., Mouton, A.M. Radio-telemetry of pike (*Esox lucius*) in the river Yser. Gepresenteerd op 'De Startersdag in het Natuur en Bosonderzoek', 16 maart 2012, Brussel, België.

Pauwels, I.S., Goethals, P.L.M., Coeck, J., Mouton, A.M. Radio-telemetrie van snoek (*Esox lucius*) in de IJzer. Studiedag Provinciale Visserijcommissie West-Vlaanderen, 13 juni 2012, Diksmuide, België.

Pauwels, I.S., Coeck, J., Goethals, P.L.M., Mouton, A.M. Habitatgebruik en preferentie van adulte snoek (*Esox lucius*) in de IJzer. Gepresenteerd op 'De Startersdag in het Natuur en Bosonderzoek', 29 maart 2014, Brussel, België.

Project rapporten

Pauwels, I.S., Everaert, G., Goethals, P.L.M. 2010. Ecologische voorspellingsmodellen: Onderzoek met behulp van voorspellingsmodellen voor de ecologische toestand van

watersystemen als instrument voor de ex ante evaluatie van maatregelenprogramma's. Studie in opdracht van de Vlaamse Milieumaatschappij. VMM.ADD.002.2009, pp. 196.

de la Haye, M.A.A., Verduin, E.C., Everaert, G., Goethals, P.L.M., Pauwels, I.S., Blom, C., 2011. Scoren met natuurvriendelijke oevers, oevers langs regionale M-typen wateren. Grontmij, Nederland. Rapportnummer: 275711 GM-1032497/MDH, pp. 88.

Goethals, P.L.M., Pauwels, I.S., De Pauw, N., Jaarsma, N., Klinge, M., Grimm, M., Puts, T. 2012. Status, ecologie en bescherming van de snoek (*Esox lucius*) in Vlaanderen. Eindrapport TWOL Project nr. B&G/14/2012, studie in opdracht van het Agentschap voor Natuur en Bos. Universiteit Gent, Gent, pp. 111.

Organisatie van wetenschappelijke meetings en conferenties

‘Ecologische modellering ter ondersteuning van de toepassing van de Europese kaderrichtlijn water.’

Gepresenteerd op het 7e Internationale congres van “The Ecological Informatics Society”, 13-16 december 2010, Gent, België. Organisatoren: Goethals, P.L.M., Pauwels, I.S. en Everaert, G.

Gepresenteerd op de onderzoeksgroep Ecotoxicologie en Aquatische Ecologie, 2 juni 2010, Gent, België. Organisatoren: Goethals, P.L.M., Everaert, G. en Pauwels I.S.

Onderwijsactiviteiten

Practica aan de Universiteit Gent

Van 2009-2013:

Eco-technologie (Prof. Dr. Ir. Peter Goethals): Praktische oefeningen en gastlessen voor Master in de Bio-ingenieurswetenschappen, (24 uur)

Aquatische ecologie (Prof. Dr. Ir. Peter Goethals): Praktische oefeningen en excursies voor Master in de Bio-ingenieurswetenschappen (28 uur)

Waterkwaliteitsbeheer (Prof. Dr. Ir. Peter Goethals): Praktische oefeningen en excursies voor MSc. Environmental Sanitation and Technology en Master in de Bio-ingenieurswetenschappen, Engelstalig programma (36 uur)

Begeleiding van scripties en stages

Steffie Van Nieuland (2010-2011). Thesis: Ontwikkeling en toepassing van een ruimtelijk expliciet en dynamisch model van snoek in rivieren. Master in de Bio-ingenieurswetenschappen, Universiteit Gent. Promotoren: Goethals, P.L.M., Mouton, A.M., Begeleiders: Pauwels, I.S., Baetens, J.M.

Pieterjan Verhelst (2011). Thesis. Paaimigratie van snoek (*Esox lucius* L.). Bachelor in de biologie, Universiteit Gent. Promotoren: Goethals, P.L.M., Mouton, A.M., Begeleidster: Pauwels, I.S.

Wouter De Lie (2011-2012). Thesis en stage: Ecologische analyse van de Burggravenstroom. Bachelor in de Chemie, optie Milieuzorg, KaHo Sint-Lieven, Gent. Promotoren: Goethals, P.L.M., Van Overschelde, R., Begeleidster: Pauwels, I.S.

Mieke Van De Walle (2011-2012). Thesis: Ecologische analyse en evaluatie van de Burggravenstroom volgens de Europese Kaderrichtlijn Water. Master in Environmental Sanitation, Universiteit Gent. Promotoren: Goethals, P.L.M., Van Verre, M., Begeleidster: Pauwels, I.S.

Laura Courteyn (2011-2012). Thesis: Migratie- en draagkrachtanalyse van snoek (*Esox lucius*) in de IJzer en de Burggravenstroom. Master in de Bio-ingenieurswetenschappen, Universiteit Gent. Promotoren: Goethals, P.L.M., Mouton., Begeleidster: Pauwels, I.S.

Angelo Kwitonda (2012-2013). Thesis: Biomonitoring and assessment of urban streams in Kampala, Uganda. Master in Environmental Sanitation, Universiteit Gent. Promotoren: Goethals, P.L.M., Begeleidster: Pauwels, I.S.